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A Study of Prairie Deer-Mouse Populations in Southern Michigan

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Introduction

The present study was undertaken with the purpose of obtaining statistically significant quantities of information about the populations and the movements of the prairie deer-mouse. Data on several other phases of the life history of the species also have been obtained incidentally.

A field study of the prairie deer-mouse *(Peromyscus maniculatus bairdii)* by the use of a live-trapping technique was conducted during the field seasons of 1938 and 1939. This is one of several similar studies initiated under the direction of L. R. Dice. Strunk (unpublished thesis) studied the home ranges of the meadow vole *(Microtus p. pennsylvanicus)*, and originated the technique of setting live traps in a grid pattern on measured plots. Burt (unpublished manuscript) in working with the wood-mouse *(Peromyscus leucopus noveboracensis)* developed the technique that largely has been used in the present study. An important contribution was his method of trapping a given area during regular periods (usually one week) alternating with similar periods in which no trapping was done.

Workers at several other institutions also have used live traps in studying small mammal populations. Chitty (1937) worked in England with the field mouse *(Apodemus sylvaticus)* and bank vole *(Clethrionomys glareolus)*. Dalke and Sime (1938) studied the home range of the cottontail *(Sylvilagus*

floridanus mallurus). Hamilton (1937a, 1937b) has worked mostly with the meadow vole. Allen (1939) used live traps to study the cottontail *(Sylvilagus f. mearnsii)* in southern Michigan.

All of the field work was conducted on the Edwin S. George Reserve of the University of Michigan, in Livingston County, Michigan. The investigations in the 1938 season extended from March 29 to September 27, but the author was in the field continuously only from July 4 to September 27. In 1939, the period of field work extended from April 23 to September 23, and the author was mostly in the field on alternate weeks after May 23.

The facilities of the George Reserve were made available by F. M. Gaige, Director of the Museum of Zoology. B. J. Bujak and P. F. Blair, Jr., served as field assistants during a part of the 1938 season. I am indebted to the former for certain data pertinent to my study obtained by his use of nest boxes in the fall of 1938 and 1939. I am indebted to W. H. Burt for suggestions while planning the field investigations. Irving J. Cantrall kindly made available the identifications of plants which were made by Fred Hermann, of the United States Bureau of Plant Industry. The part of the field work concerned with the determination of the breeding rate of the deer-mouse was supported by a grant from the Michigan Academy of Science, Arts, and Letters.

Methods

In the 1938 season, plots 1, 3, (Fig. 1 and 2) and 4, comprising about 7.6, 9.0, and 3.8 acres, respectively, were trapped. In 1939, plot 4 again was trapped, and plot 1 was changed somewhat and enlarged to about 9.0 acres. The shift in plot 1 was made necessary by a pond that formed in one end due to an artificial change in the drainage. In addition to the regular trapping areas, in 1938, some 40 to 50 acres elsewhere were trapped for short periods and at various intervals, in an attempt to retake mice that moved from the regular plots.

In calculating the size of the plots, one-half the distance between two trap lines has been added on those sides where the blue-grass association extended beyond the limits of the trapping areas. Thus the calculated size of each plot is somewhat larger than the area on which the traps actually were set. This method has been used to minimize the error resulting from some mice having ranges that extend beyond the limits of the trapping area.

Small live traps of the single-catch type were used, and only one trap was placed at a spot. Most of the traps were of wooden construction, but some were made of copper. The wooden traps were superior to the metal for everything except the meadow vole, which often gnawed them severely. The traps were set in parallel lines. In the lines the traps were placed 60 feet apart. On two of the plots and on about one-third of another, the lines were 60 feet apart; on the remaining area, they were only 45 feet apart. Two principal considerations guided the spacing of the traps on the plots. It was necessary to space the traps closely enough to catch all of the resident animals and to give reliable data on the size of the individual home ranges. On the other hand, it also was necessary to place the traps sufficiently far apart that, with

the personnel available, it was possible to trap relatively large areas. The spacings used proved a very satisfactory compromise, and also worked quite well for the wood-mouse, meadow vole, jumping mouse, and short-tailed shrew. Each trap on the regular plots was left in the same spot during the season's trapping.

The traps were baited with a mixture of millet, hemp, wheat, and canary seed. Each trap was provided with a small wad of cotton that could be utilized by the mouse for building a nest. The traps were set in the evening, usually between 5 and 7 o'clock. They were visited in the morning, usually between 7 and 9 o'clock. The traps were left unset during the day to prevent spermophiles from getting in them and dying from the heat. In the summer of each season the plots were trapped during alternate weeks. This method of spacing the trapping periods gives the residents of each plot a week to recover from the disturbances and possible deleterious effects of the previous week of trapping. During the spring, the trapping periods varied in length, because the weather was so cold much of the time that the mice would have died in the traps.

Each mouse was numbered by clipping one toe off a forefoot and by punching holes in the ears. In a few cases the hole in the center of an ear later would be torn out to the edge, apparently by snagging or through fighting. In spite of this, however, the numbers of such mice usually could be recognized. Each mouse was released at the point where it was taken, after its sex, approximate age, breeding condition, and the number of the trap in which it was caught had been recorded.

In the field notes the deer-mice were separated into 4 age groups. Those still completely in juvenile pelage were classified as immature. Those in part juvenile and part adult pelage were called subadult. Those in adult pelage, but definitely young animals, were classified as young adult. All others were considered adult. For purposes of summarization, the immature and subadult classes have been combined in the present report.

The statistical computations are by M. A. Taylor. Standard errors rather than probable errors are used. In the comparison of two means the border line of significant difference between the two is considered to be 2.7 or more times the standard error of their difference (see Dice and Leraas, 1936).

Ecological Associations

The prairie deer-mouse normally occurs on the George Reserve only on grassy areas, on which the principal dominants are two species of blue-grass (*Poa compressa* and *P. pratensis*). The former species is by far the most important herb on the well drained soils of the uplands, and in many places it forms almost pure stands. The latter species occurs on poorly drained soil in the swales and along the moist margins of ditches and ponds, where it generally is more luxuriant than *compressa* of the uplands. The amount of admixture of other herbs with the blue-grass on various parts of the Reserve apparently depends on the past history of the respective areas. Most of plot 1, which has a relatively pure, dense stand of blue-grass, is on a rather steep

slope, and so far as known was never cultivated. However, it probably was utilized as grazing land. Plots 1 and 3, according to local residents, were cultivated before 1900, and today these plots have a greater variety and abundance of herbaceous species than plot 1. Other than blue-grass, the most conspicuous plant on the upland parts of plot 1 is common milkweed *(Asclepias syriaca)*. Some of the other herbs characteristic of plot 3 and 4 are found there, but they are not abundant. A panic grass *(Panicum scribnerianum)* is present in some abundance on a level area of well drained soil, in plot 1.

Plot 1 differs from the other regular trapping areas in having a considerable area of poorly drained soil with a luxuriant growth of herbs and some shrubs. In this situation, characteristic plants are: shrubby cinquefoil *(Potentilla fruticosa)*, bur marigold *(Bidens discoidea)*, boneset *(Eupatorium perfoliatum)*, swamp thistle *(Cirsium muticum)*, Canada thistle *(Cirsium arvense)*, timothy *(Phleum pratense)*, golden-rod *(Solidago graminifolia)*, black-eyed susan *(Rudbeckia hirta)*, and yarrow *(Achillea millefolium)*.

On plots 3 and 4, and less abundantly on the better drained parts of plot 1, the principal herbs in addition to the blue-grass are: common milkweed, yarrow, common mullein *(Verbascum thapsus)*, silvery cinquefoil *(Potentilla argentea)*, panic grass *(Panicum scribnerianum* and *P. tennesseense)*, wild bergamot *(Monarda fistulosa)*, pearly everlasting *(Anaphalis margaritacea)*, pussy's toes *(Antennaria neglecta* and *A. neodioica)*, galingale *(Cyperus filiculmis)*, daisy fleabane *(Erigeron ramosus)*, bush clover *(Lespedeza hirta)*, dropseed *(Sporobolus neglectus)*, and pinweed *(Lechea minor)*. Both plots 3 and 4 have small patches of sweet clover *(Melilotus alba)*. On one end of plot 3, there is some shrubby smooth sumac *(Rhus glabra)*. On this same plot, there is one large black oak *(Quercus velutina)*, and one black cherry *(Prunus serotina)*. There also is a small gully with a dense growth of shrubby dogwood (*Cornus* sp.).

All of the grassy areas studied are considered, for the purpose of the present study, to be parts of the blue-grass association. On the George Reserve, the areas of blue-grass association alternate with oak—hickory woodlots. Each of the trapping areas, consequently, was bordered on two sides by the oak—hickory association. Plot 4 was bounded on a third side by a cornfield that adjoined the Reserve. On the other sides, the blue-grass association extended beyond the limits of the study areas.

Most of the small mammals of the blue-grass association are shown in Tables 1, 2, and 3. Of these, the wood-mouse *(Peromyscus leucopus noveboracensis)*, and the chipmunk *(Tamias striatus lysteri)*, are principally forest inhabitants, and the latter occurs in the blue-grass association only as a casual invader. The short-tailed shrew *(Blarina brevicauda talpoides)*, meadow vole *(Microtus p. pennsylvanicus)*, and jumping mouse *(Zapus h. hudsonius)*, are most abundant in the moistest parts of the association. Species that are known to range over the association, but were not taken in the traps, include: the common mole *(Scalopus aquaticus machrinus)*, striped skunk *(Mephitis mephitis nigra)*, red fox *(Vulpes fulva)*, and deer *(Odocoileus virginianus borealis)*.

TABLE 1.—Catches of small mammals on plot 1, E. S. George Reserve, Livingston County, Michigan

1938	Peromyscus manículatus bairdii	Peromyscus leucopus noveboracensis	Microtus p. pennsylvanicus	Blarina brevicauda talpoides	Zapus h. hudsonius	Synaptomys c. cooperi	Tamias striatus lysteri	Mus musculus	Citellus t. tridecemlineatus	Mustela frenata noveboracensis	Total
March 29-April 1	3	..	..	..	..	..	..	..	..	..	3
April 19-22	4	1	..	..	..	..	..	..	..	..	5
May 11-14	8	..	..	..	..	..	..	..	..	..	8
May 21-23	8	2	3	..	..	..	..	..	..	..	13
June 15-20	15	8	10	..	..	..	..	..	..	..	33
July 11-17	12	21	41	3	..	..	1	..	..	..	78
July 25-31	13	21	31	9	..	1	..	..	..	..	75
August 9-16	14	19	37	12	..	3	..	..	..	..	85
August 24-30	12	11	33	8	..	5	..	..	..	..	69
September 7-13	9	6	38	13	1	4	..	..	..	..	71
September 21-27	12	11	28	17	..	5	..	1	..	..	74
1939											
April 23-26	2	3	..	..	..	..	..	..	..	..	5
May 23-29	3	10	..	..	1	..	..	..	..	..	14
June 8-15	2	16	1	2	16	..	..	..	..	..	37
June 24-30	..	15	..	1	29	..	..	..	..	1	45
*July 9-17					20						
July 23-29	2	9	1	..	25	..	..	..	2	..	39
August 6-12	1	10	1	4	23	1	..	..	1	..	41
August 20-26	..	8	..	7	13	1	..	..	1	..	30
September 3-9	..	8	..	4	8	..	..	..	1	..	21
September 17-23	..	4	..	6	15	1	..	..	..	..	26

* Traps set only on part occupied by jumping mice.

TABLE 2.—Catches of small mammals on plot 3, E. S. George Reserve, Livingston County, Michigan.

1938	Peromyscus manículatus bairdii	Peromyscus-leucopus noveboracensis	Microtus p. pennsylvanicus	Blarina brevicauda talpoides	Citellus t. tridecemlineatus	Tamias striatus lysteri	Zapus h. hudsonius	Synaptomys c. cooperi	Mus musculus	Total
April 20-22	8	2	..	..	..	..	..	..	..	10
May 11-14	10	3	..	..	2	..	..	..	..	13
May 21-23	10	4	..	..	8	..	..	..	..	16
June 15-20	15	14	2	..	8	1	..	..	..	39
July 4-10	16	26	2	..	4	..	1	..	..	53
July 18-24	18	27	6	1	4	..	..	2	..	56
August 1-8	12	19	2	..	3	..	..	1	..	37
August 17-23	20	16	14	..	1	1	..	2	1	53
August 31-Sept. 6	20	10	6	..	..	..	..	1	..	38
September 14-20	20	13	14	..	..	..	..	2	1	50

TABLE 3.—Catches of small mammals on plot 4, E. S. George Reserve, Livingston County, Michigan

1938	Peromyscus maniculatus bairdii	Peromyscus leucopus noveboracensis	Microtus p. pennsylvanicus	Blarina brevicauda talpoides	Zapus h. hudsonius	Tamias striatus lysteri	Total
July 10-16	32	6	..	1	..	2	41
July 24-30	35	8	..	1	..	..	44
August 9-15	29	6	..	1	..	..	36
August 24-30	14	6	..	..	..	..	20
September 7-13	19	5	2	..	..	..	26
September 21-27	22	5	2	2	..	..	31
1939							
April 23-26	14	3	..	..	..	..	17
May 23-29	8	8	..	..	..	..	16
June 8-15	10	11	..	..	..	..	21
June 24-30	9	9	..	..	..	..	18
July 23-29	11	14	..	..	1	..	26
August 6-12	10	10	..	..	..	..	20
August 20-26	10	8	..	..	..	..	18
September 3-9	8	7	..	..	..	..	15
September 17-23	7	2	..	..	..	..	9

Populations

The deer-mouse was found to be the most abundant small mammal of the blue-grass association. The meadow vole, jumping mouse, and short-tailed shrew also were numerous at times in some parts of the association. Data that were obtained on the meadow vole, jumping mouse, and short-tailed shrew have been previously reported (Blair, 1940, a, b, and c, respectively).

POPULATIONS OF SMALL MAMMALS

A comparison of the total catches of small mammals on the three study areas (Tables 1, 2, and 3) shows that most of the species of small mammals were common to all of them. The relative abundance of the different species, however, differed considerably on each plot. On plot 1 in 1938, the meadow vole was the most abundant mammal, and the deer-mouse was the next most plentiful resident species. The wood-mouse, which ranged from contiguous woods into the edges of the area, however, outnumbered the deer-mice during several of the trapping periods. On plot 3 in 1938, the order of abundance was reversed, and the deer-mouse exceeded the meadow vole in numbers. The wood-mice during some periods outnumbered on this plot both the deer-mice and the meadow voles. Spermophiles were fairly numerous in this area, while none was taken on plot 1. On the other hand, short-tailed shrews were much scarcer than on plot 1. On plot 4 in 1938, the prairie deer-mouse was by far the most plentiful mammal; the numbers of wood-mice were proportionally smaller than on the other plots; and other species of mammals were relatively scarce.

In 1939, the proportions of the various species differed from those in the previous year. On plot 1, the deer-mouse comprised a minor part of the population. The jumping mouse was the most abundant species, in contrast with its scarcity the preceding year. The meadow vole was extremely scarce, whereas it had been the most plentiful form in 1938. On plot 4, in 1939, the deer-mouse still was the most abundant small mammal, although the numbers of wood-mice were greater than during the previous year and approximately equalled those of the deer-mice. Other species were even scarcer than in 1938.

Plots 3 and 4 were nearest alike in the proportions of the several species of small mammals making up their populations. In these two plots most of the environmental features were fairly similar. Most of the area of both plots was relatively dry blue-grass association, which favors the deer-mouse. Both plots were bordered by woods from which wood-mice ranged into the blue-grass association. The greater numbers of wood-mice on plot 3 than in plot 4 apparently were due to the much longer woods—grass border. The marked dissimilarity of plot 1 evidently was caused by the presence there of a considerable amount of relatively moist blue-grass association and the contiguity of extensive areas of marshland. These moist situations, virtually lacking on the other plots, account for the relatively great abundance in plot 1 of the meadow vole, jumping mouse, and short-tailed shrew.

These data indicate that, at least in the two years of the study, the prairie deer-mouse was the most abundant small mammal on the relatively dry parts of the blue-grass association on the George Reserve. On and near the moist parts of the blue-grass association, the deer-mouse was less abundant than the meadow vole in 1938, and scarcer than either the jumping mouse or the short-tailed shrew in 1939.

Populations of Deer-mice

The catches of deer-mice on the trapping plots are shown in Tables 1, 2, and 3, and the calculated numbers per acre on each plot are shown in Table 4. It is evident that the concentrations of deer-mice were not the same on the different trapping areas. Plot 4, which was smaller than either of the others, consistently had the greatest gross catch and the greatest average number of deer-mice per acre in both years. Plot 3 usually had more mice than did plot 1, although the difference was not nearly so great as between 1 and 4.

A definite seasonal cycle of abundance was noticeable on each plot in both years, except on plot 1 in 1939 when the population was very small and eventually vanished. In the early spring, the population was small and made up of adults that survived the preceding winter. These animals began to breed in the spring, and those of their offspring that survived increased the population until a maximum was reached about the last of July. Then the concentration of deer-mice tended to decrease as many of the mice ceased breeding during the middle of the summer. It increased again in late summer and autumn, after the autumn breeding season began. During the winter, the population decreased to a spring minimum. It is interesting that on plot 4 in 1939 the largest population of the year was found in April. By late May,

however, all but 5 of the 13 adults had disappeared, presumably through movement into other areas. Thereafter, the seasonal cycle followed the general pattern, although it was less pronounced than in 1938.

During no two trapping periods were exactly the same individuals present on any of the plots. The individual deer-mice taken on plot 3 during each trapping period in 1938 are shown in Table 5. There were certain resident animals that remained in the area throughout most of the trapping season. Examples on plot 3 are males No. 1847, 1848, and 1857, and females No. 1825, 1826, 1842, 1890, and 1900. Each of the other plots also had certain residents that remained throughout most or all of the trapping season. On plot 4, a female that was first taken about mid-July, 1938, remained there during the remainder of the trapping season, and also was on the same plot through the 1939 season. This particular individual apparently, therefore, remained in the same general locality for at least 15 months, if we assume that it remained there during the winter when no trapping was done. Some residents disappeared at irregular times from the plots. Several of these later were taken on other plots, indicating a movement from one plot to another. Others never again were taken, indicating that they either fell victim to predators or that they moved beyond the study areas. Some previously uncaught adult animals moved onto the plots, and a few moved through but failed to remain there. A few individuals left the plots, then returned after rather long absences. Examples on plot 3 are male No. 1815, which returned after an absence of about 4 months, and female No. 1816, which returned after an absence of about two months (Table 5). The young deer-mice taken either matured and remained on the plots, or they disappeared after one or two trapping periods. Some of those that disappeared later were taken in other plots, but others never were retaken. These data indicate that during the seasons studied the deer-mouse populations on a given area are continually changing. Some individuals remain for long periods of time; others disappear, and still others move in. Young animals mature to increase the adult population, or move away, or possibly are victims of predators, disease, or accident.

Because the field work has extended over only two seasons, the data on annual fluctuations in abundance are limited. There was a very marked decrease in deer-mouse abundance from 1938 to 1939. On plot 4, the average number per acre dropped from 9.2, the 1938 maximum, to 2.9 per acre at a comparable time in 1939. On plot 1, the concentration of deer-mice decreased from a maximum of 2.0 per acre in mid-June of 1938, to a maximum of only 0.3 per acre in late May, 1939. No deer-mice were living on the plot in the last part of the 1939 season. On plot 3, which was under observation by Bujak in 1939, the deer-mice were scarcer than during the previous year. Possibly the dry spring and consequent failure of much of the blue-grass to set seed accounted for the small populations of deer-mice in 1939.

Winter Carryover

The average life of a deer-mouse in nature on the George Reserve is less than one year, although individuals of another subspecies of the deer-mouse,

kept in the laboratory, have lived for 7 and 8 years (Dice, 1933:147). When trapping was begun on plot 1 in April, 1939, not a deer-mouse remained of those I had marked there in 1938. One of the two mice recorded in late April, 1939, had been born in the fall of 1938 and was marked then by Bujak; the other was unmarked, and, therefore, presumably was born after trapping was discontinued in 1938. On plot 4, only two of the 13 adult deer-mice present in late April, 1939, had been residents of the plot during the previous summer, having been born in early summer of 1938. Of the other 11 mice, 5 are definitely known to have been born on the plot in the fall of 1938, and the others presumably were born then, as they were unmarked. Thus, most of the residents of the plot in 1938 had disappeared by the beginning of the 1939 breeding season. The population in the spring of 1939, therefore, was mostly made up of mice that had been born during the previous fall. Consequently there was an almost complete annual turnover in population.

The concentration of deer-mice varied on the different plots, but even on the most densely populated area the greatest average number per acre was only 9.2 individuals. There is a definite seasonal cycle of abundance. The relatively small spring population increased to a maximum in about late July; there was some decrease in numbers as sexual activity slowed during mid-summer; the population increased after the fall breeding got under way; then there was a decrease during the winter. There is evidence of marked annual fluctuations in abundance, for the deer-mice were much scarcer in 1939 than in 1938. The deer-mice surviving the winter were mostly those that had been born in the previous fall, indicating an almost complete annual turnover in population.

TABLE 4.—Average number of prairie deer-mice per acre on the trapping plots in 1938 and 1939.

	Average No. Per Acre Plots				Average No. Per Acre Plots	
1938	1	3	4	1939	1	4
March 29-April 1	0.4	Not trapped	Not trapped	April 23-26	0.2	3.7
April 19-22	0.5	0.9		May 23-29	0.3	2.1
May 11-14	1.0	1.1		June 8-15	0.2	2.6
May 21-23	1.0	1.1		June 24-30	....	2.4
June 15-20	2.0	1.7		July 23-29	0.2	2.9
July (first period)	1.6	1.8	8.4	August 6-12	0.1	2.6
July (second period)	1.7	2.0	9.2	August 20-26	....	2.6
August (first period)	1.8	1.3	7.6	September 3-9	....	2.1
August (second period)	1.6	2.2	3.7	September 17-23	....	1.8
September (first period)	1.2	2.2	5.0			
September (second period)	1.6	2.2	5.8			

TABLE 5.—Trapping periods in which each individual deer-mouse was caught on plot 3 during 1938 season. o indicates transient; + indicates immature; × indicates adult and young adult.

Field No.	Trapping Periods									
	April 20-22	May 11–14	May 21–23	June 15–20	July 4–10	July 18–24	August 1–8	August 17–23	Aug. 31- Sept. 6	Sept. 14–20
♀										
1812	×	×		×						
1816	×				×					
1825	×	×	×	×	×	×	×	×		
1826	×	×	×	×	×	×			×	×
1830		×(dead)								
1842		+	×	×	×	×	×	×	×	×
1845			×	×	×	×	×	×		
1844			+			×→(moved 1150 feet away)				
1890	(from 865 feet away)→			×	×	×	×	×	×	×
1899				×	×	×		×		
1900				+	×	×	×	×	×	×
1910				+	+	×	×	×	×	
2079						o				
2048						+				
2270								+	+	×
2190						(from 1320 feet away)→			×	×
2337						(from 330 feet away)→			o	
1896						(from 410 feet away)→			×	×
2349									+	+
2408										+
♂										
1814	×									
1815	×	×								
1721	→o (from 660 feet away)									
1824	×	× (dead)								
1828		× (dead)								
1831		×								
1832		×	×	×						
1847			×	×	×	×	×	×	×	×
1857			×	×	×	×	×	×	×	×
1848			+		×	×	×	×	×	×
1898				×						
1870			×	×	×	×				
1914				+	+					
1949					×					
1946					+	+	+	×→(moved 825'away)		
1889			(from 825 feet away)→			×	×	×		
2049						+				
2116							×	×	×	×
2139					(from 3795 feet away)→			×	×	
1946(a)								×		
2267					(from 1730 feet away)→			×		
2225								+		
2263								+	+	+
2276								+	+	×
1897						(from 410 feet away)→			×	
2359									×	×
2361									+	+
2412										+
2414										+

Home Ranges

One of the principal objects of the field study was to determine the average size of the home range of the prairie deer-mouse. The method of calculating home range size already has been described (Blair, 1940a). With this method, one-half the distance between two traps is allowed beyond the outermost traps in which each mouse is caught. This obviously does not show the exact shape and size of the individual home ranges, but the figure thus derived is believed to approximate the actual area of the home range.

The sizes of the home ranges have been calculated on a monthly basis. Each monthly home range is based on the records from the two alternate weeks of trapping during the month. The ranges have been calculated on this monthly basis, because of the occasional movements of the mice. A deer-mouse sometimes would have a definite home range in some particular locality, but later it would move to a new home range on the same or on another plot. Therefore, in order not to confuse movements with home range it was necessary to restrict the period for which the home range would be calculated. It was possible, at best, to catch any one mouse 14 times during a month. Some individuals were taken every night, but most were caught less frequently. In many cases the calculated home range included some traps in which the individual mouse was not taken during the month. In large ranges the number of traps within the calculated range exceeded the possible number of catches per month, so the fact that the mice did not get into every trap within their respective ranges does not seem particularly significant. Nor does it appear to detract from the validity of this method of calculating the area of the home range.

Not all of the deer-mice were caught a sufficiently large number of times during a month to give adequate information about the size of their respective home ranges. Some apparently transient individuals were caught only once. Also, some residents that disappeared shortly after the beginning of a trapping period might have been caught only once or twice, and immigrants that took up residence near the end of a trapping period also might be caught only a few times during that trapping period. In order to exclude such incomplete records from the calculations of home range size no home range based on less than three catches per month is used. Another problem has been the elimination of home ranges that were only partially within the plots near edges where the blue-grass association extended beyond the trapping areas. Many of these are eliminated by excluding from the calculations ranges based on less than three catches per month. In addition, all mice that were taken in not more than two adjacent traps near an edge bordered by blue-grass association also have been excluded from the calculations.

A total of 153 monthly home ranges of prairie deer-mice have been calculated according to this method. Seventy adult males that were caught an average of 7.0 times each per month had an average monthly home range comprising 0.63 $\pm$ .04 acre, while 64 adult females that were caught an average of 7.1 times each per month had an average monthly home range of

0.51 ± .04 acre. There is no significant difference in the size of the male and female ranges, the difference in the means being 0.12 ± .06 acre. The largest female range comprised 2.29 acres on plot 3 in August, 1938, but only one other female range exceeded one acre. The smallest female range comprised 0.12 acre on plot 1 in August, 1938. The largest male range was 1.67 acre on plot 3 in September, 1938, the smallest 0.25 acre on plot 3 in July, 1938.

Ten home ranges of immature males, based on 5.4 catches per individual per month, averaged 0.61 ± .11 acre. The largest comprised 1.37 acre on plot 3 in July, 1938, and the smallest comprised 0.08 acre on the same plot in September, 1938. Nine home ranges of immature females, also based on 5.4 catches per individual per month, averaged 0.64 ± .09 acre. The largest comprised 0.99 acre on plot 3 in September, 1938, and the smallest 0.17 acre on plot 4 in July, 1938.

The home range of each deer-mouse tends to remain in the same vicinity over a rather long period of time, although the shape and size as computed by my method vary more or less from month to month. Each adult, therefore, generally remains on the same part of the plot as long as it stays on that plot. Examples of the length of residence of individual deer-mice on a plot are shown in Table 5. The longest that one individual apparently resided in the same home range was about one year. This female on plot 4 occupied during the 1939 season almost identically the same home range that it had during the summer and fall of 1938. If we may assume that the female stayed in the same area during the intervening winter, it is apparent that she occupied approximately the same range for about a year. The entire area that this female ranged over during the year, as indicated by the trapping records in the two seasons, comprised only 0.53 acre, which was only slightly larger than her largest monthly home range of 0.49 acre in July, 1938. This is an extreme case, of course, and most of the deer-mice remained in their respective home ranges for shorter periods of time.

The fluctuations from month to month in the shape and size of the calculated individual home ranges possibly are due to limitations of the trapping technique which allows at best only 14 catches during a month. I am inclined to believe, however, that the home range of a deer-mouse is not a definite bit of terrain with fixed limits. Instead, the home range is undoubtedly a constantly changing unit that varies with the changing needs of the individual mouse. The size and shape of the home range over which an animal habitually ranges probably are conditioned by many factors, particularly: (1) location of the home site or home sites, (2) available food, (3) distribution of preferred cover, (4) location of temporary refuges, (5) relations to other individuals of the same sex and species, (6) relations to individuals of the opposite sex of the same species, (7) relations to individuals of other species, (8) weather, (9) micro-climates.

Most of these factors change from time to time. The available food and cover, for instance, change with seasonal changes in the vegetation. At times

of great abundance of food a mouse would have to range only a short distance from its nest to feed, but at times of scarcity it might have to range over a relatively large area. The relations of a sexually active individual to others of the same species undoubtedly are different from those of a non-breeding animal. With these changes in the determining factors the size and shape of the home range must also continually change.

The home range of each deer-mouse usually overlaps that of one or more other individuals of the same or of opposite sex. This overlap occurs at times of low concentration of deer-mice as well as at times of high. When the species is abundant in an area the amount of overlapping naturally is greater than when the species is scarce. The greatest overlapping of home ranges was found on one end of plot 4 in 1938. There in July, 1938, on an area comprising about 0.77 acre, the home ranges of 8 resident adult females and of 4 resident males broadly overlapped. In the following month 5 adult females and 4 males had similarly overlapping ranges in the same area. In September, 5 adult female and 4 male ranges overlapped in the area. One of the females was suckling young in July and in August, and all of the females apparently were pregnant in September. The home ranges of various breeding females likewise broadly overlapped in other parts of the same plot and on the other plots. This indicates that, in the prairie deer-mouse of southern Michigan, there is no antagonism and consequent territorial behavior among breeding females similar to that described by Burt (1940) in the wood-mouse. A striking example of the overlapping of the ranges of two breeding female deer-mice on plot 3 is shown in Figure 2. Females No. 1826 and No. 1842 occupied ranges that were largely coincident. Both were sexually active at this time as evidenced by the fact that the latter bore a litter on September 19 and another on October 16, and the former gave birth to young on October 6.

Even though a great many of the home ranges overlapped, there usually were some vacant spaces on the plots in addition to the vacant zone bordering the woods into which the deer-mice seldom ventured. The smallest amounts of vacant space were found on plot 4 in 1938, when deer-mice were abundant there. There were virtually no parts of the plot, except along the border of the woods, that were not included within the home range of one or more male or female deer-mice. On plot 4 in 1939 and on plot 1 and 3 in 1938, with relatively small populations of deer-mice, there were, in each month, rather large areas from which one or the other sex was absent and smaller areas that were not in the home ranges of either sex (see Figs. 1 and 2).

In general, the data on home ranges of the prairie deer-mouse indicate that in southern Michigan the average home range of both immature and adult males and females comprises about one-half acre. The home range of each individual tends to remain in the same vicinity over a rather long period of time. There is some month to month fluctuation in the size and shape of the calculated home ranges, apparently due to differences in the daily movements of the individual mice produced in turn by their changing vital needs. The

home range of each deer-mouse usually overlaps that of one or more individuals of the same or opposite sex. This is true of breeding as well as non-breeding mice. Notwithstanding the overlapping, there usually are some unoccupied spaces in the plots.

Refuges

During the 1938 season several of the deer-mice and wood-mice were followed after being released from the traps until they entered holes or found other places of refuge. Most of the mice showed by their actions that they knew the terrain well, and they went directly to a hole or other refuge. On several occasions an individual used the same route when going from a trap to a refuge. In a very few cases a mouse acted as if lost when released from

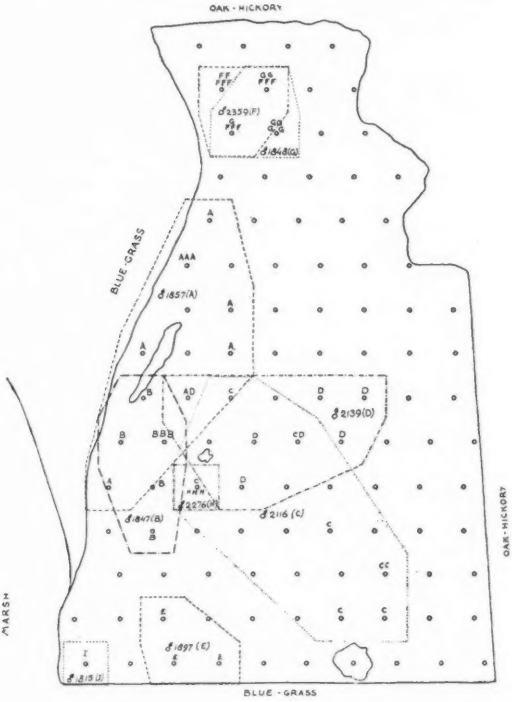

Fig. 1. Home ranges of adult male deer-mice on plot 3, September, 1938. Letters indicate traps in which each individual was caught and the number of times it was caught in each. Broken lines show the limits of the calculated home ranges.

the trap. In some cases a mouse would appear lost for a few moments, and would run a few feet away from the trap. Then, apparently becoming oriented, it would reverse direction and go directly to a hole. From my observations of the released mice it seems certain that each individual generally knows well the terrain within its home range, and that each tends to follow certain definite trails. In many cases the mice were lost to sight in heavy blue-grass or other relatively dense vegetation, so the holes they entered could not be located. However, enough mice were followed to definite holes or other refuges to give a fairly reliable indication of the types of refuges that they sought. Some of the holes to which the mice went probably were their "permanent" homes, but others probably were only temporary refuges. From the evidence at hand, therefore, it may only be said that all of the holes to which the mice went served as refuges at a time of danger, and that presumably some of the holes were the actual homes of the mice.

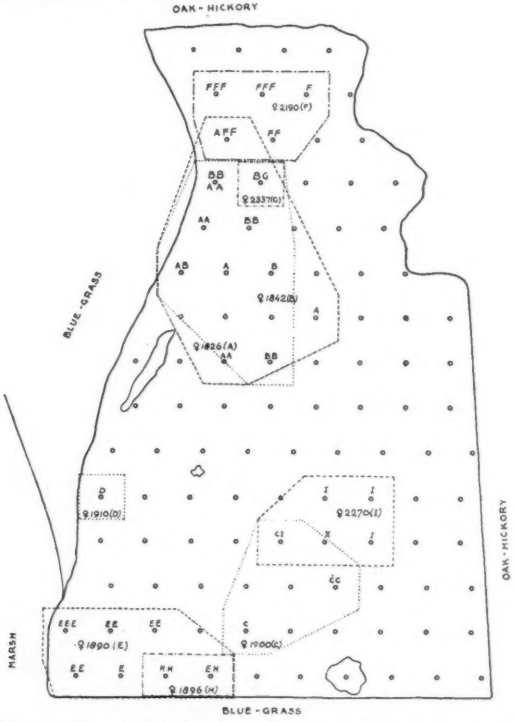

Fig. 2. Home ranges of adult female deer-mice on plot 3, September, 1938. Letters indicate traps in which each individual was caught and the number of times it was caught in each. Broken lines show the limits of the calculated home ranges.

Fifty-seven deer-mice were followed to some refuge or other a total of 113 times. The mice went 45 times to small holes that they apparently had made themselves. They went 42 times to spermophile holes. All of the spermophile holes apparently had been previously abandoned by their makers. The deer-mice went 18 times to old tunnels of the common mole. In 4 cases the mice went to logs in the blue-grass association. In three cases they went to old, abandoned skunk dens. One deer-mouse went to an abandoned fox den. Thus 40% of the times the deer-mice went to holes that they apparently had made, while 57% of the times they went to the abandoned holes and tunnels of other mammals. Only three per cent of the times did they go to logs.

Usually the refuge to which a deer-mouse fled was located within the limits of its home range determined from the trapping records. A total of 123 records of the distances traveled by deer-mice before they reached a refuge or were lost to sight in dense vegetation are available. In 114 (93%) of these cases the deer-mouse did not leave its home range. In 7 (5%) of the cases the mouse went less than 30 feet beyond the limits of the plotted home range, and in only 2 (2%) of the cases did a mouse go more than 30 feet beyond the limits of its known home range. The fact that in 93% of the cases the mice did not leave their calculated home ranges and in another 5% of the cases went less than 30 feet beyond the calculated range supports my belief that the ranges calculated according to my method represent fairly accurately the actual ranges of the mice.

The number of refuges which an individual deer-mouse might have within its home range is indicated by the data on some of the mice. An adult female during July, 1938, went to 4 refuges within its home range. Two were spermophile holes, and two apparently had been dug by the mouse. The mouse went to one of the spermophile holes on two different occasions. In August the same individual went to 6 different refuges within its home range, which then partially overlapped its July range. However, all of the refuges were different from those used during July. Four of the 6 were spermophile holes, and two apparently had been made by the mouse. One of the spermophile holes was used twice. The refuges were fairly evenly distributed over the home range, so the mouse when it was in any part of its range had a possible refuge near at hand. An adult male in August went to 5 different refuges, of which 4 were within its calculated home range, and one was about 15 feet beyond. Four of the 5 were spermophile holes, and one apparently had been made by the mouse. One of the spermophile holes was used twice. The August home ranges of the male and female discussed above overlapped broadly, but neither went to a refuge to which the other went. During August the home ranges of two other adult females overlapped this area. One of these females went to three different refuges, one of which also was used by the male discussed above, but on a different date. The other female went to one refuge, which also was used by the first female, but on a different date. Thus in this particular area there were at least 13 separate refuges used by the resident deer-mice. In most cases only one individual went to a particular refuge, but two females

went to the same refuge at different times, and to another refuge a male and female went at different times.

In July, 1938, an area of sand with an extremely sparse cover of panic grass *(Panicum)* and scattered oak seedlings and clumps of prostrate juniper was trapped. Several of the deer-mice went directly to clumps of juniper. When other of the deer-mice in this area were released they traversed barren situations as rapidly as possible, and often instead of finding a hole they stopped in the shelter of a seedling or clump of grass. Field notes on two representative individuals indicate the type of behavior in this area:

Adult ♀2044, July 22, 1938, went 12 feet west from trap 96 to base of oak seedling 8 feet in height; sat up and nonchalantly washed face.

Young adult ♀2042, July 18, 1938, ran 10 feet from trap 64 to shrubby oak; could hardly be routed from beneath it; ran around and around base of oak; finally ran out and under clump of panic grass; when routed out there ran back to base of oak.

As long as the mouse remained beneath the oak seedling it would be relatively safe from attack by a winged predator, which probably would, on the other hand, have little difficulty in catching it if it ventured out onto the barren sand. The reluctance of the mice to leave such cover as that of the oak seedlings seemed to indicate their recognition of its protective value.

In this sandy area, too, was taken the only deer-mouse that entered even the edge of the woods when released from the trap. This individual, a young, adult male, was unable to find a hole in the grassland and went 96 feet to the edge of the woods. At the wood's edge the deer-mouse climbed three feet up the trunk of a large tree but fell off. Then it hid among the dead leaves on the ground. En route to the woods, the mouse stopped under juniper seedlings and other cover, but I chased it away from such cover each time it stopped. The deer-mouse did not go directly to the woods, but apparently encountered the woods by accident due to my chasing it there.

Twenty-nine wood-mice were followed to some refuge in the blue-grass association a total of 43 times. Many other times the wood-mice went into nearby woods, but they were not followed to their refuges there. The wood-mice went only 10 times to holes in the blue-grass association that they apparently had themselves made. Eleven times they went to stumps in the blue-grass association, and one wood-mouse went to a log there. The wood-mice went 16 times to mole tunnels, and 5 times they went to abandoned spermophile holes. It is obvious from these data that the wood-mouse, when it ranges into the blue-grass association, sometimes utilizes the same types of abandoned mammal burrow used by the deer-mouse. In areas where the two species occur together there is, therefore, the strong possibility of competition between them. The wood-mice tend to utilize stumps and logs when those are available in the blue-grass association, but they certainly are not limited to this type of refuge.

In general, these observations on the released mice show that each deer-mouse and each wood-mouse generally knows the terrain within its home range and has little difficulty in finding a hole or other refuge at a time of apparent danger. Both the deer-mouse and wood-mouse use some holes that they

apparently have themselves made, and both also utilize the abandoned holes and tunnels of other mammals when these are available. As both species tend to use the same type of refuges there possibly is competition for refuges and home sites when the two animals occur in the same area. In areas of sparse cover the deer-mice sometimes take refuge beneath tree seedlings and other scattered bits of cover from which they can hardly be forced away. Most of the deer-mice that were followed after being released from the traps went to refuges within their calculated home ranges. A deer-mouse may have 6 or possibly more refuges within its home range. Where several individual mice occupy the same area, the abundance of refuges may be still greater.

Movements

The movements of individual deer-mice onto and from the plots played an important part in altering the concentrations of the species on each of the study areas. The data on these movements give some indication of how far adult deer-mice move, when for some reason or another they leave one home-site and seek another. They also show, in a few cases, how far a deer-mouse moves from its birthplace before settling down and, in turn, reproducing. In addition to the normal movements of the mice on the regular study plots, other movements were produced experimentally by increasing and decreasing, respectively, the populations on certain areas.

Invasion of a Sparsely Populated Area

One field experiment was performed to determine the rate and extent to which deer-mice would occupy an area from which most of the original population of deer-mice had been removed. In this experiment a plot was laid out in the midst of an area of relatively uniform blue-grass association. This plot was 540 feet long and 360 feet wide, and the area enclosed by the outer trap lines comprised 4.46 acres. The area from which the mice were removed actually was somewhat larger than this, because some of the mice undoubtedly had home ranges that extended beyond the outer lines of traps. Seventy traps were set in this plot. They were spaced 60 feet apart in lines that were the same distance apart.

This plot was trapped for 6 days, to determine the original population, and all of the mice taken during this period were marked and released. On the three succeeding days, all of the deer-mice taken were removed. The mice were removed on only three days, because it was feared that if they were removed over a longer period some invading mice also would be taken off. As it was, 5 previously unmarked mice were taken on the last day of trapping. These quite possibly were invaders, but one could not be certain about this. so they were removed. The total number of deer-mice marked on the plot during the 9 days of trapping was 47, of which 25 were adult males, 20 were adult females, and two were immature females. Five of the adult males and a like number of the adult females were not removed, as they were not taken during the last three days of trapping. One adult male wood-mouse was marked, but it was not removed. After the mice had been removed from this

plot the population of deer-mice per unit area undoubtedly was smaller than in contiguous areas of the same association type.

The plot was left undisturbed for one week, and at the end of that time a seven-day period of trapping was begun. During this trapping period, all of the mice taken were marked and again released. The total number of deer-mice taken during this period was 25. Of these, two were previously-marked males that had not been removed, and 11 were unmarked adult males that were assumed to be invaders; three were previously-marked but unremoved females, and 7 were unmarked females that were considered invaders; and two were immature males that may or may not have been born in the plot. The one adult male wood-mouse was retaken, and two unmarked adult males were caught.

The plot was left undisturbed for another week, and at the end of that time a final seven-day period of trapping was begun. A total of 24 deer-mice was taken during this period. The same two original males and three original females that were taken during the preceding trapping period were recaptured. Seven of the 10 invading adult males that were marked during the preceding trapping period were retaken, and three unmarked adult males also were captured. Four of the 7 invading adult females that were marked during the preceding period were retaken, and one unmarked female appeared. The two immature males marked during the preceding period were retaken, and two unmarked immature females were caught. One unmarked adult male wood-mouse was captured, but neither the original adult male nor either of the two previously-marked wood-mouse invaders was recaught.

Of the three original adult males and two original adult females that were neither removed from the plot nor taken there during subsequent trapping periods, the later history of only one is known. This was an old adult male that moved almost three-fourths of a mile south to plot 3 and settled there. It was last in plot 7 on August 5, and was first taken in plot 3 on August 17. Any reason for its movement away from plot 7 would be mere conjecture. However, it is possible that the old animal was unable to compete with the invading mice, and thus was driven out.

In the experiment described above, deer-mice moved in to occupy an area from which most of the original population of deer-mice had been removed. The invasion of the plot was quite rapid, and most of it had taken place by the end of two weeks after the original population had been depleted. In the following two weeks very little change in the population took place. The population after the invasion of the depleted area was only about one-half as great as the original population. The results of this experiment indicate that there is a tendency, at least at the time of the year that the experiment was conducted, for deer-mice to move quickly into sparsely-inhabited areas of suitable habitat types.

Colonization

The population of deer-mice on plot 1 was very small in 1939. There were only two individuals, an adult male and a female, during the period from April 23 to 26. When the area next was trapped, from May 23 to 29,

the female had disappeared, and no female deer-mouse was taken on the plot during the rest of the 1939 season. In the May period, the adult male still was on the plot, as were two immature males, presumably offspring of the adult pair. One of the immature males moved away to plot 4 between May 29 and June 8. The other immature male disappeared after June 11, and the adult male disappeared after June 14, leaving the plot barren of deer-mice. No deer-mice subsequently were caught on the plot until late July, when one immature male moved there from three-fourths of a mile to the north, and one previously unmarked immature male moved onto the area. The formerly marked male is known to have stayed 6 nights, and was last taken on July 29. One week later it appeared in plot 4. The other male remained until early August. On August 8 this mouse was taken on the plot, but on August 9 it was caught on plot 4. On August 10 and 11, it was back in plot 1, but after this it moved again to plot 4 and stayed there at least until the end of trapping in late September. After this individual left, no other deer-mouse was taken on plot 1.

The invasion of the two males that were first taken in late July clearly was an attempted colonization of the unpopulated plot. The colonization probably failed because no females moved onto the area. The two males lingered for a time on the plot, then moved on to plot 4 where there were both males and females. The disappearance of the adult and of the two immature males earlier in the summer probably is attributable also to the lack of females on the area, after the one resident female had disappeared between late April and late May, possibly through predation, disease, or accidental death. The populations of deer-mice were small on all of the areas under observation in 1939, and the population pressure consequently was low. The low population pressure, resulting in little dispersal, probably accounted for the failure of the deer-mice to successfully colonize plot 1. Bujak reported that a pair of deer-mice was living on the plot in October, thus indicating an apparently successful later colonization of the area.

Dispersal from an Over-populated Area

An experiment was performed to determine the amount, rate, and distance of dispersal of deer-mice from an over-populated area. For this experiment it was necessary to create a supposedly over-populated condition by introducing a large number of deer-mice into an area of blue-grass association already occupied by the species. A relatively isolated field comprising 2.9 acres of blue-grass association was selected. This area was bordered on the north and south by oak—hickory forest and on the east and west by marshes, so that it was separated from other similar areas of blue-grass association (Fig. 3).

The selected area was trapped for four night (August 6 to 9) to determine its original population. One adult male and one adult female constituted the deer-mouse population. There also was a population of 14 adult male, 14 adult female, and one immature male wood-mice. Most of the wood-mice apparently ranged into the grass area from the contiguous oak—hickory association.

Forty-five deer-mice, of which 22 were adult males, 19 were adult females, and four were immature females, were released in the area at 7:30 p.m. on August 9. Thirty-seven of the 45 mice had been removed from the depopulation plot, which was about two-thirds of a mile north of this area. The other eight had been in captivity at the Laboratory of Vertebrate Genetics in Ann Arbor, where four of them were born. The other four, one of which was the parent of the laboratory born animals, came originally from the George Reserve. After the mice were released in the area the population of deer-mice per unit area was much larger than the maximum in other parts of the George Reserve.

Following the release of the mice the area was left undisturbed for a week. The area in which the mice had been released was then trapped for one week (August 17 to 23). During this period three adult male, four adult female, three immature male, and two immature female deer-mice were taken. Two of the mice were the original pair, and four of the immature animals apparently were their offspring. The others were mice that had been liberated on the area. There also were 34 wood-mice and one short-tailed shrew. The plot was left undisturbed the following week. Then the final period of trapping (August 31 to September 6) was begun. During this time, the same seven adult deer-mice that had been taken in the previous trapping period were

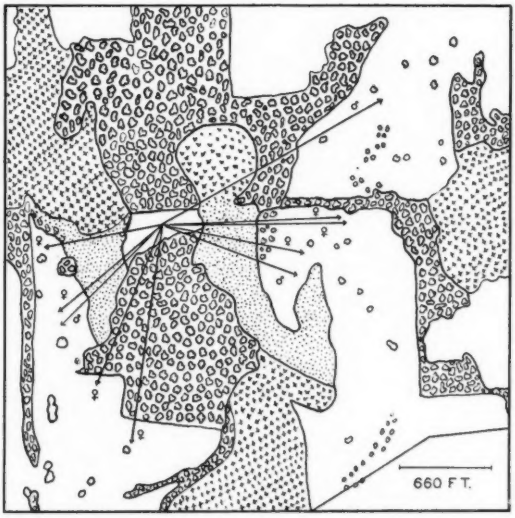

Fig. 3. Dispersal of deer-mice from artificially over-populated plot. Each arrow points to place a mouse was recaptured. Blank spaces indicate blue-grass association; stippling, marsh; crosses, swamp; small crenulate symbols, oak-kickory. Note that most of the mice apparently moved through the marshes.

caught, but three of the immature mice had disappeared. There was an additional population of 23 wood-mice, two short-tailed shrews, and one jumping mouse. These data make it evident that only a few of the mice released on the plot remained there, while most of them apparently were forced to seek other homes or were captured by predators. The population of deer-mice that remained in the area apparently was the maximum population that could maintain itself successfully there under the existing conditions of environment and probable competition with the wood-mice.

An attempt was made to determine the fate of the 39 released mice that were not retaken on the plot by trapping areas of blue-grass association on all sides of the plot. All of the areas of blue-grass association shown in Fig. 3 and some additional areas to the north and east were trapped at various times during the second, third, and fourth week after the release of the mice. The plot from which most of the mice originally were taken also was trapped, but none of them returned to it. The 10 mice that were recovered outside of the plot on which they had been released were retaken at distances of from 825 to 1815 feet from the point of release. The average distance from the point of release to the point of capture was 1228 feet or almost one-fourth of a mile. The fact that only three of the recaptured animals were males while seven were females possibly signifies that the males tend to travel farther than the females and thus moved out beyond the trapping areas. In moving out from the over-populated area the mice probably traveled considerably greater distances than the actual distance in a straight line between the point of release and the point of recapture. The location of the points at which the mice were retaken suggests that they probably traveled through the marshes to the east and west (dry at that season) in moving away from the over-populated plot. With the six individuals that remained in the plot, the recovery of 10 mice outside of the area gives a total recovery of 16 (35%) of the 45 mice that were released. The other 29 mice apparently were taken by predators, or possibly traveled such great distances that they were not retaken in the areas trapped.

From this experiment it is evident that there is a tendency for deer-mice to spread away from an over-crowded area until the population becomes sufficiently reduced that it can survive under the existing environmental conditions. Such a condition of over-population probably seldom occurs in nature, because a continuous tendency for dispersal eliminates surplus individuals from an area.

Movements of Adult Deer-mice

After the resident populations had been trapped on plots 1, 3, and 4 in 1938 and on plot 4 in 1939, a total of 30 other adult deer-mice moved onto the plots during the course of the seasons' trapping. Thirteen of these were unmarked, and apparently came from areas on which no trapping was done. The other 17 (57%) either moved from one of the three plots to another or moved from nearby areas on which the resident mice had been marked during short periods of trapping. In addition to these, some adult mice moved out of the plots and were recovered elsewhere. In all, there are 30 cases in which

the distance of movement of an adult deer-mouse from one home range to another is known. Twelve males moved an average of 1168 feet, or a distance equal to about 7.0 times the width of the average male home range. Eighteen females moved an average of 758 feet, or about 5.1 times the width of the average female home range. The greatest distance that an adult male moved was equal to about 22.9 times the width of the average male range. This movement was an exception to the general rule, however, since most of the males moved a distance of less than 10 times the width of the average male range. The greatest distance that an adult female moved was equal to about 8.9 times the width of the average female range.

The available data do not represent random samples of movements of adult deer-mice, because some of the mice that moved onto the plots obviously came from beyond the limits of the trapping areas. Likewise, some of the mice that moved from the plots probably traveled beyond the limits of trapping. The greatest distances of movement, therefore, probably are not represented by these data. It is evident from these records, however, that a majority of the adult deer-mice that move from one home range to another travel a distance of not more than 10 times the width of an average home range. It also is indicated that the males tend to move farther than the females.

Movements of Immature Deer-mice

The data on the movements of the young deer-mice are not particularly enlightening because, when an immature mouse was first caught, there usually was no way of knowing whether it had been born in the vicinity or whether it was an immigrant. Of 36 mice that were first recorded on the plots as immature, 20 (56%) remained there at least until they were adult, while 16 (44%) disappeared from the plots before they were adult. Some were recovered outside of the regular plots, indicating movement of at least some of them. Of the immature mice that reached maturity on the plots, all except one remained as adults in the same vicinities where they were taken as immatures. One female moved about 300 feet from where she was taken as an immature and remained in that general area.

The distances that 6 immature males and 4 immature females moved are known. The distances that the males moved varied from about 500 feet to about 3960 feet, and averaged 1334 feet. The immature male that moved the greatest distance was born in the laboratory at Ann Arbor and was one of several adult and immature deer-mice released on August 14, 1939, about three-fourths of a mile north of plot 1. Ten nights later it was taken on plot 1. This animal traveled a distance equal to about 24 times the width of the average home range of an adult male. The distances that the immature females moved varied from 180 to 1030 feet, and averaged about 453 feet.

Spring Dispersal

Ten deer-mice that spent the winter of 1937-38 in a nest box on plot 1 apparently were a pair and two litters of offspring born in the fall of 1937 (see Nicholson, unpublished manuscript). This group, comprising the parental

pair with 5 male and 3 female offspring, was in the nest box on March 6, 1938. At this time the parental female and one other female were brought into the laboratory to find if they were pregnant, but they failed to produce any young. On March 13, only the parental male was in the nest box, but on March 19 and 28 one of the female offspring was with him. On the latter date, the two captive females were released in the vicinity of the nest box. The male is known to have remained in the vicinity of the nest box until mid-June. He was absent from the plot during July and most of August, but reappeared in late August and remained in the same vicinity at least until the end of trapping in late September. One of the female offspring remained in the vicinity of the nest box until May 23, and in the meantime produced a litter. Another female offspring occupied, until May 13, a home range of which the approximate center was about 100 feet from the nest box.

The other 7 deer-mice apparently moved away from the plot, and 4 of them were retaken elsewhere. The three unaccounted for possibly were taken by predators or possibly moved beyond the limits of the trapping areas. The 4 taken elsewhere all were males. Three of these moved about 650 feet, or almost 4 times the width of one average male home range, onto another plot. One remained there only until May 14, after which it disappeared, and another remained until mid-June. The third, however, remained until late August. One male was taken on plot 3, about 650 feet from the nest box, but it was caught only once and therefore it presumably moved on through this plot.

It is interesting that after this aggregation broke up in the spring a majority of the mice settled, at least for a time, within not more than about 4 times the width of an average home range of the nest box in which they spent the winter.

In the spring of 1939, I suspected that there was a movement of deer-mice away from plot 4 before the beginning of the major part of the breeding season. In the period from April 23 to 26, 13 adult and one immature deer-mice were caught on this plot. When the area was next trapped from May 23 to 29, only two of the adult males and two of the adult females remained. None of the 10 others ever again was taken. The decrease in population was by far the greatest that was observed in a similar length of time, and seems to have been too great to attribute to predation. No trapping was done, however, in most of the nearby areas into which the mice might have moved, so there is no definite evidence that the mice did move away. It is interesting that never during the following summer did the population on the plot become as large as the population of 13 adults that carried over from the previous fall and was present in late April.

Inbreeding

The data on the aggregation of 10 mice found in a nest box in the spring of 1938 give some information on the possible amount of inbreeding in the prairie deer-mouse. The parental male that remained in the vicinity of the nest box was found there in association with one of the female offspring on March 19 and 28, and with another daughter on March 29 and April 18. The

first female gave birth to three young about April 8. As the parental male was associated with the daughter at about the time these young were conceived, and no other male was known to be in the vicinity, it seems quite probable that the young were the result of a father-daughter mating. There is no evidence that the other daughter produced any young as a result of association with the father, as this female disappeared after April 18.

The litter that resulted from the circumstantially evident father-daughter mating comprised three females. One of these never was taken after it left the nest, but the two others settled on the plot and stayed during most of the summer and bore young there. Both females established themselves about 180 feet, or slightly more than the width of one average female home range, from the nest box in which they had been born. One produced one litter there in June, by July had moved to another range about 300 feet from the nest box, and after July disappeared from the plot. The other remained in her range about 180 feet from her birthplace throughout the summer and produced two litters there. At no time did the calculated range of either female overlap that of her father-grandfather. In August, the range of one female extended to within 60 feet of the range of the male, and in September it extended to within 30 feet of the male range. With the ranges of the two in such close proximity there would be a possibility of a mating of the female and her father-grandfather. It seems most probable, however, that a male of unknown parentage, that occupied an overlapping home range, was the father of the litters produced by this female.

In general, young deer-mice tend to move away from the vicinity of their birthplace before settling down, and in turn reproducing. Some individuals, however, may remain near the nest and there mate with other members of the same family.

TABLE 6.—Percentage of adult female deer-mice breeding, E. S. George Reserve, Livingston County, Michigan (all females pregnant, suckling, or recently suckling considered to be breeding).

1938	Total Examined	Breeding	1939	Total Examined	Breeding
March 29-April 1	2	1 (50%)	April 23-26	8	6 (75%)
April 19-22	6	4 (67%)	May 23-29	6	6 (100%)
May 11-14	6	6 (100%)	June 8-15	2	1 (50%)
May 21-23	7	2 (29%)	June 24-30	2	2 (100%)
July (first period)	14	2 (14%)	July 23-29	5	3 (60%)
July (second period)	31	7 (23%)	August 6-12	5	2 (40%)
August (first period)	27	11 (41%)	August 20-26	5	5 (100%)
August (second period)	22	11 (50%)	September 3-9	2	1 (50%)
September (first period)	22	19 (86%)	September 17-23	2	2 (100%)
September (second period)	18	14 (78%)			

Breeding Rate

The breeding season and the number of litters produced by one female during the breeding period were determined mostly by examining the females that were trapped in the field. The average number of young per litter was found by capturing pregnant females away from the trapping areas and keeping them until their young were born, and by counting the number of young in litters that were born in the nest boxes.

Breeding Season

An immature female, taken March 30, 1938, evidently was born about March 5. Most of the breeding, however, began somewhat later. Four immature deer-mice, all caught in the same vicinity between April 19 and 21, probably were members of a litter born about the first of April. Another immature, caught elsewhere on April 22, probably was born about April 1. A female, captured March 30, had a litter on April 4. As the trapping on about 20 acres of blue-grass association resulted in the capture of only one immature deer-mouse before mid-April, the evidence proves that very few young were produced before the first of April. On March 4, 1939, 13 males and 12 females were examined in Bujak's nest boxes. Four of the males had enlarged testes; one female possibly was pregnant, and two others had the vagina open. On March 19, 1939, three of 5 males examined had enlarged testes; one of 10 females possibly was pregnant, and 4 others had the vagina open. An immature, caught April 19, and another caught in the same vicinity on April 25 probably were members of a litter born about the first of April. An immature, caught May 22, probably was born about April 15 to 20. Four immatures, caught in the same vicinity on May 22, probably were members of a litter born about May 1. It is evident that in both 1938 and 1939 few young were born before early April, although in the former season one litter was produced as early as March 5.

The close of the breeding season is shown by the nest box records of Bujak, as my trapping was discontinued before the end of the fall breeding. In 1938, the last known litter was born on October 30. In 1939, the last known litter was born about November 6. Therefore, the time of close of the breeding season in the fall was about the same in both years, just as the beginning of the spring season was approximately the same. In both seasons, the time of the breeding season from the beginning in spring to the close in the fall was about 7 months.

Although the breeding season extended over about 7 months, not all of the females were breeding all of the time. Table 6 shows that in 1938 a large percentage of the females were sexually active in the spring and fall, but that there was relatively little breeding in mid-summer. In 1939, the females were much scarcer and did not show such a marked mid-summer slump. The seasonal breeding cycle is quite different from that found in another subspecies, *artemisiae*, in central Washington by Scheffer (1924:258). He found the deer-mice breeding throughout the year, with the largest percentage of pregnant females in January, June, and November.

Size of Litters

Forty-three litters of the prairie deer-mouse have been examined. The smallest number in a litter was one and the largest was 6. The average number of young per litter was 4.0 ± .2. The standard deviation was 1.3 individuals. The average number per litter in the wild mice was almost the same as the average number (4.04 ± .03) per litter found by Svihla (1932:26) in 179 litters of laboratory stocks of deer-mice belonging to 6 subspecies.

Sex Ratio

Of the 333 prairie deer-mice examined in 1938, 170 (51%) were males, and 163 (49%) were females. In 1939, 65 individuals were caught, of which 36 (55%) were males, and 29 (45%) were females. This indicates that the sex ratio is about even.

Age of Breeding

The approximate date of birth and the approximate date of first parturition in nature of 17 female deer-mice are known. These animals were residents on the plots, and consequently were under observation from shortly after leaving the nest until after the beginning of sexual activity. Three females became sexually active at the age of about 6 weeks, and produced their first litters at an age of about 9 weeks. One female did not conceive young until she was about 18 weeks old, and consequently did not produce a litter until she was around 21 weeks of age. The average age at which the females first conceived was 9.5 ± .8 weeks. These data agree, on the whole, with the findings of Clark (1938) in laboratory stocks of the species *maniculatus*, for he found the average age of attainment of sexual maturity of females to be about 7 weeks, and the age of first conception to be from 5 to 10 weeks. The average age of first parturition in the field animals was around 12 weeks. The males apparently became sexually active at about the same age as the females. Numerous young males born in the spring were sexually active the following summer and fall. The youngest breeding male examined was still in juvenile pelage and was estimated to be from 5 to 6 weeks old. In this individual the testes were enlarged and located in the scrotum.

Number of Litters per Year

The females that were breeding during mid-summer (Table 6) were mostly those that had been born the preceding spring. The females born in late spring and in the summer usually have from one to three litters before the end of the breeding season; and probably average about two. The old females that have carried over from the previous fall and those born early in the spring may have as many as 4 litters during the year. As a general rule, the old females produce two litters in the spring, two others in the fall.

Rate of Increase

Knowing that old females produce about 4 and young females about two litters during the 7-month breeding season and knowing the average number of young per litter to be 4, and the sex ratio to be about even, one can calculate the theoretical rate of increase of the species. Given one pair of adult deer-mice at the beginning of the breeding season, with the female bearing two litters in the spring and two in the fall, and spring-born females producing two litters each in the fall, the original pair would have 48 descendants at the end of the breeding season. This assumes, of course, that all of the female offspring survive and reproduce, which probably happens very rarely in nature.

Number of Young on the Plots

The probable numbers of young that were born on each plot can be estimated from the data on the breeding condition of the females. During the 1938 trapping season, the 14 adult females that resided at one time or another on plot 1 apparently produced 10 litters or 40 young mice that should have left the nest before the end of the trapping season. Only 24 immature and young adult mice were actually taken in the traps, leaving 16 (40%) of the estimated young unaccounted for. In the same period the 15 adult females that resided at one time or another on plot 3 apparently gave birth to 8 litters or 32 young individuals. Of this number, 25 were trapped, leaving only 7 (22%) of the expected number unaccounted for. In the 1939 trapping season on plot 4, the sexual condition of the 7 adults that resided there at one time or another after the spring dispersal, indicated that about 11 litters or 44 young mice were produced in time to leave the nest before the end of the trapping. Only 11 immature and young adult mice were trapped, however, leaving the fate of 33 (75%) unknown. The discrepancy between the estimated numbers produced on the plots and the numbers of young actually recorded probably is due mostly to mortality. Dispersal, however, may have been of some importance. There was some movement of young mice from one plot to another, and possibly some of them moved away from the trapping areas. It seems probable, however, that movements out of the plots would have been offset by movements of other young into them. The relatively low survival rate on plot 4 in 1939 possibly is significant, in view of the failure of the populations in that year to become nearly so large as in 1938. The females definitely were reproducing, but few of the young survived, and the populations consequently failed to increase very greatly.

Relations to the Wood-Mouse

No deer-mouse ever was taken in the woods on the George Reserve during all of the time that Burt (1940) was trapping there, nor during the time that I trapped in the woods there. In fact the home ranges of the deer-mice very rarely extended even to the edge of the woods (Fig. 4). In four cases the calculated home ranges of deer-mice extended nearly to the edge of the woods, since the mice were taken in traps that were set within about 30 feet of the nearest tree branches. One deer-mouse had a home range that extended on both sides of a row of trees. With these exceptions, the home ranges of

the deer-mice did not approach the border of the woods, and there always was a strip of grass along the woods border (measured from the nearest branches) in which the deer-mice were not taken. On plot 3 in 1938 this strip averaged 129 feet wide in July, 136 in August, and 127 in September. On plot 4 in the same year this strip averaged only 40 feet wide in July, 46 in August, and 43 in September. The concentration of deer-mice was much greater on plot 4 than on plot 3, and the resultant greater population pressure probably caused the deer-mice on plot 4 to range closer to the woods than did those on plot 3. This hypothesis is supported by the fact that in 1939, when the deer-mouse population on plot 4 was much smaller than in 1938, the average width of the strip in which the deer-mice did not occur was 78 feet in June, 93 feet in August, and 84 feet in September. From these data, the general statement

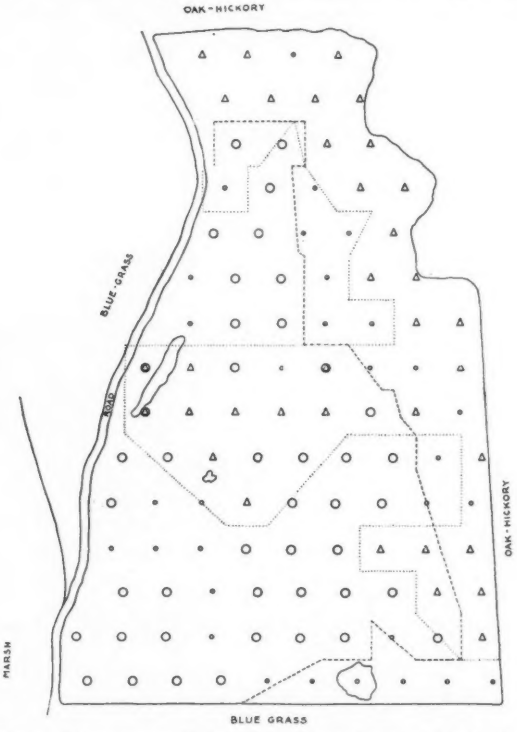

Fig. 4. Limits of home ranges of deer-mice and wood-mice on plot 3, August, 1938. Large circles indicate traps in which deer-mice were caught, triangles those in which wood-mice were taken. Small circles show traps in which neither species was obtained. Broken line shows limit of deer-mouse home ranges in direction of woods. Dotted line shows outer limits of wood-mouse ranges in grass.

may be made that on the George Reserve the prairie deer-mouse, so far as we know, never inhabits forest situations. Furthermore, there is a zone of grassland, where the grassland is bordered by forest, into which the deer-mouse seldom ranges. This zone is known to vary in width from about 40 to 130 feet, and its width at any given time probably is conditioned by the population pressure in the deer-mouse population at that time.

The wood-mouse primarily is an inhabitant of woodland associations in southern Michigan. However, wood-mice were taken both years on every grass plot, along the edges bordered by the oak—hickory association. Where there were no trees or brush in the blue-grass association the ranges of the wood-mice extended out about 125 feet into the blue-grass association bordering the forest. In plot 3 in July, 1938, the average extension of the wood-mouse ranges into the blue-grass association was 123 feet, and in August it was 120 feet. In September, the wood-mouse ranges extended out into the grass along only about three-fifths of the woods—grass border. Where the wood-mice did range out their ranges extended out an average of only 93 feet. Thus there was an indication that the wood-mice ranged into the blue-grass association less extensively in September than in July and August. On plot 4 in the same year a similar drop was noted in September. In July the wood-mice extended out an average of 108 feet into the grass, and in August they extended out an average of 141 feet, but in September they extended out an average of only 66 feet. In 1939 the ranges of the wood-mice extended about the same distances onto plot 4 as in 1938, the average being 138 in June, 111 in August, and 123 in September. However, it is noteworthy that there was no drop in September such as occurred on both plots in 1938. It seems likely that the distance the wood-mice ranged into the grassland is correlated with the amount of population pressure in the woodlots. However, the concentration of wood-mice in the various woodlots at those seasons are not known, so no attempt can be made to correlate the population pressure of the wood-mouse with its extension into the grass.

In July and August of 1938, the wood-mice ranged about 450 feet across a part of plot 3 to a small ravine in the grassland occupied by low dogwood (*Cornus* sp.) and a few shrubby elms (Fig. 4). The situation here is somewhat different from that of the wood-mice ranging from the woods into purely grassy situations. In this case they ranged from a woodlot across grass to a small island of a forest type of habitat. A part of the wood-mice lived in the vicinity of the brushy ravine, and others ranged between it and the forest bordering the opposite side of the plot. In the vicinity of the ravine and in the blue-grass association between the ravine and woodlot the home ranges of the wood-mice broadly overlapped those of the deer-mice. Along most of the woods border in plot 3, however, there was little or no overlap of the ranges of the wood-mice and deer-mice. On plot 4 the ranges of the two species overlapped more broadly than they did on plot 3. The data at hand do not satisfactorily show the relationship between individuals of the two species. However, they do indicate that on the George Reserve the wood-mice range out from the woodlots into a strip of the adjacent grass about 125 feet

wide which they occupy largely to the exclusion of the deer-mice. There is, nevertheless, some overlapping of the ranges of the two species along the outer edge of this strip, and where the wood-mice occur around isolated areas of brush and trees in the grassland the ranges of the two overlap broadly.

Home-ranges of Wood-mice

There was a small woodlot, comprising a little less than two acres between plots 1 and 4. Wood-mice were caught in the grass bordering this plot in both 1938 and 1939. Therefore this wooded area was trapped for 10 nights during June, 1939, to determine if the wood-mice recorded from the grass ranged also into the woodlot. Four adult female, three adult male, and three immature wood-mice were taken in the woodlot. All of these individuals also were taken in the nearby grass and no other wood-mice were taken there. Thus it is evident that each wood-mouse in the vicinity ranged over some forest and over some grass. The average home range of the 10 wood-mice in June comprised 0.81 $\pm$ .15 acre. The largest home range was that of an adult male and comprised 1.50 acre, and the smallest was that of an adult female and comprised 0.30 acre. On the average, the 10 wood-mice had home ranges of which 25% of the area was in the forest and 75% was in the grass. The fraction of the calculated range in the forest is not absolutely comparable with that in the blue-grass, however, for there were only 10 nights of trapping in the forest compared with 14 in the grass. Only one individual had more of its known range in the forest than in the grass. This was an immature female that had 54% of its range in the forest. An adult male had 5% of its range in the forest and 95% in the grassland. These data should not be taken to indicate that the home range of any wood-mouse necessarily must include both grass and forest, but they do indicate a tendency for the wood-mice to range over both grassland and forest where the two are in contact. Also, where there are limited areas of forest surrounded by larger areas of grass more of the range of an individual wood-mouse sometimes is in the grass rather than in the forest. The home ranges are much larger than those calculated by Burt (1940) for wood-mice in the forest, and although few in number, seem to indicate that the animals tend to range more widely when they occur in grass than when in forest associations.

Summary

The prairie deer-mouse *(Peromyscus maniculatus bairdii)*, on the Edwin S. George Reserve, Livingston County, Michigan, normally occurs only in the blue-grass association.

The abundance of deer-mice per unit area varies from place to place in the blue-grass association. There is a definite seasonal cycle of abundance, correlated with the breeding cycle. The breeding population in the spring is mostly made up of animals that were born in the previous fall, which indicates an almost complete annual turnover in population. The deer-mice were much scarcer in 1939 than in 1938, indicating fluctuation in abundance from one year to the next.

The average home range of an adult female deer-mouse, in this area, comprises about 0.51 ± .04 acre, while that of an adult male makes up about 0.63 ± .04 acre. The home range of each adult deer-mouse usually remains in the same vicinity over a relatively long period of time. The shape and size of each individual range tends to fluctuate. The home range of each deer-mouse usually overlaps that of one or more individuals of the same and opposite sex. There is no evidence of antagonism between breeding females; in fact, two or more such females sometimes occupy almost identical home ranges.

If the population of deer-mice is removed from an area in the midst of a large expanse of blue-grass association, other deer-mice tend to move in from the surrounding area. When, on the other hand, a large number of deer-mice are liberated in a given area, most of them tend to move away from the over-populated point of release. Young deer-mice usually move away from their birthplace as they mature, and adult mice sometimes move away from established home ranges. All of these movements apparently are due to population pressure.

The breeding season of the deer-mouse, in southern Michigan, extends from about the first of April to the last of October. More females usually are breeding in the spring and fall than during the summer. The average number of young per litter is 4.0 ± .02 individuals. The sex ratio is about even. Old females have an average of about 4 litters a year. The young females first conceive young at an average age of about 9 weeks, and usually produce about two litters each before the end of the same season.

Wood-mice, in this area, occasionally range into the blue-grass association, where their home ranges sometimes overlap those of the deer-mice. In this association, the two species use the same types of refuges.

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Observations on the Ecology and Natural History of Anura. II.

Habits, Habitat, and Breeding of Bufo woodhousii woodhousii (Girard) in Oklahoma[1]

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It is widely recognized that an organism can exist or thrive as a species only where it can adjust itself to prevailing conditions of the environment. But, before one can understand how this principle applies in any given case, it is necessary to determine the habits of the organism in its natural habitat. Experimental and other essentially laboratory problems must be solved befote the genetical, physiological, cytological, and embryological phases of the larger problem are known, but to understand the reactions and behavior of an animal within the complex of environmental factors among which it lives, one must still of necessity go directly to nature.

In the grasslands of North America, animals of all of the principal terrestrial groups exist whose habits have been little studied. Till recently, almost nothing was known of the Natural History of the Anura of this vast region, except whatever notes had been published concerning habits and habitats more or less incidental to essentially taxonomic and distributional studies such as those of Strecker (1902-1935) in Texas, of Smith (1934) in Kansas, of Ortenburger (1926) in Oklahoma, of Tanner (1931) in Utah, and others.

The present series of papers was planned to fill partially this wide gap in our knowledge. The first contribution (Bragg, 1940) summarized the existent knowledge concerning the Natural History of the Great Plains toad (*Bufo cognatus* Say) and compared some of its habits with those of the eastern *B. americanus americanus* (Holbrook) as reported by Miller (1909) in central Massachusetts and by Wright (1914) in New York. This, the second paper in the series, reports the result of a similar study of the Rocky Mountain toad (*Bufo woodhousii woodhousii* [Girard]), particularly as I have observed it in central Oklahoma throughout all favorable seasons during the past four years. Since the habits of this toad differ materially from those of *B. cognatus* in the region studied, it seems desirable to emphasize these differences in the following discussion.

The methods used are essentially as outlined in the former paper (Bragg, 1940), the exception being that the region studied is broader. Most of the detailed observations given concern toads inhabiting central Oklahoma, but

1 Contributions from the Zoological Laboratory of the University of Oklahoma, No. 207.

these have been supplemented by studies made in most other regions of the state during all hours of the day and night at favorable times and seasons. No less than fifteen trips to various parts of the state have been made. Breeding activities have been observed in six different counties, located in southern, central, and southwestern Oklahoma.

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History and Morphological Variations of Bufo w. woodhousii, Its Range, General Habits, and Habitat

Bufo woodhousii woodhousii was described by Girard (1856) from San Francisco Mountain, Coconino County, Arizona, and has since been reported many times from the eastern and southern Rocky Mountains, east through the Great Plains, and southwest to southern California. According to Wright and Wright (1933) its general distribution is "Montana to Texas, west to southeastern California. Great Plains and Great Basin region." Smith (1934) says, "Western United States east of the Sierra Nevadas and Cascade Range, east to western Texas, Oklahoma, Kansas, and Nebraska."

Along the poorly defined eastern limits of its range, an area of intermingling exists between this toad and several other species. Smith (1934) found specimens in eastern Kansas which approached *B. fowleri* Hinkley so closely in characteristics as to be practically identical with it. In McLennin County, Texas, Strecker (1908) found a similar integradation or other intermingling of characters among *B. woodhousii* Girard, probably *B. fowleri* Hinkley, *B. americanus americanus* (Holbrook), and rather interestingly, *B. cognatus* Say. Wright and Wright (1938) also mention this difficulty in east-central Texas.

In Oklahoma, this zone of interrelationship occurs on a line passing southwestward from Craig County in the northeast to Pushmataha and Choctaw Counties in the south. East of this zone, *B. w. woodhousii* is rare or absent except along the Arkansas River in Sequoyah County, and the common toad is *B. americanus americanus* (Holbrook). Within the zone, particularly in the southeast, it is very difficult to distinguish individual specimens as of one species or the other so closely do the two approach each other in characteristics (See Bragg and Smith, 1940, for a more extended discussion). In the northeastern quarter of the state, a variation of *B. w. woodhousii* occurs which, technically, has to be classed as *B. w. woodhousii* but which, nevertheless, is clearly recognizable as a constant variation from the more typical specimens to be found to the westward.

The specimens in question will be reported upon in detail later. At the present time, they are interpreted as *B. w. woodhousii* with some tendency toward the characters of *B. a. americanus,* particularly in size, spinocity, and markings. Of eleven at hand from Ponca City, all have immaculate venters except one which is much spotted. The protesting note of the males of this seires is of two kinds (1) the pleasing "peep" of typical *a. americanus* given consistently by some of them and (2) the lower toned, trill-like note of *w. woodhousii* given by others. Two toads differing in this manner were morphologically indistinguishable. It is possible that we are here dealing with hybrids since typical *B. w. woodhousii* have been found within a few miles and the call of the American toad has been heard within the city limits of Ponca City.

In central and southern Oklahoma, I have had no difficulty in distinguishing *B. w. woodhousii* and *B. a. americanus,* and nowhere in the state does *B. cognatus* approach either in characteristics.

The Rocky Mountain toad is abundant in most parts of Oklahoma, although it tends to be replaced by *B. a. americanus* in the eastern third of the state. I have collected it or know positively of its presence in fifty-three of the seventy-seven counties (Fig. 1), including all of the vegetational regions of Bruner (1931) and most of the biological regions of Blair and Hubble (1938). It is practically certain that this toad occurs everywhere in the state with the exception of the northeastern and southeastern corners (Bragg and Smith, 1940).

It is the dominant toad in sandy regions nearly everywhere but is exceeded in numbers in the mixed-grass prairie of central Oklahoma by *B. cognatus* (Bragg, 1940, 1940a) and in the short-grass plains of southwestern Oklahoma

Fig. 1. Distribution of *Bufo woodhousii woodhousii* by counties in Oklahoma. Small stipples indicate records for a county; large stipples indicate the presence of the variation of this subspecies which is mentioned in the text. The records are based upon over 400 specimens collected by Dr. Charles C. Smith and the author, supplemented by examination of all specimens and locality records in the University of Oklahoma Museum of Zoology and all records given in the literature cited which are considered authentic.

(Jackson, Tillman, and probably also Greer and Harmon Counties) by *Bufo compactilis* Wiegmann, which, although till recently unreported from Oklahome, is the dominant toad of the short-grass region. *B. w. woodhousii* is the only toad known on the sandy expanses of the extensive flood plains of the larger streams (at least of the Canadian River in Cleveland County and of the Cimarron River in Logan County) and it is present on the flood-plain of the Red River, bordering Texas to the south. Except in the extreme eastern part of the state, it is the common toad of low-lying bottom-lands along streams and in wooded areas generally. Of the seven species or subspecies of toads known now from Oklahoma, *B. w. woodhousii* is the most widely distributed and most versatile toad in the state.

The Rocky Mountain toad is not nearly so sensitive to dryness as other toads in Oklahoma. At several times I have found them active on the flood plains of streams or in vegetation adjacent to them on afternoons of warm bright days. Even in mid-summer with maximum temperature well over 100° F. and an evaporation rate of from 0.3 to 0.5 in., one is almost certain to find them feeding beneath street-lights in the evenings. During the exceptionally dry fall of 1938, I consistently found them out at night during a period of three weeks throughout which I searched in vain for a single specimen of *B. cognatus* in a region (Norman, Okla.) known to contain thousands.

Smith (1934) gave a description of this toad as it occurs in Kansas which fits the specimens which I have seen in Oklahoma quite well except for some minor variations in certain specimens. In comparing *B. w. woodhousii* with *B. a. americanus*, for example, he states in regard to the former "cranial crests frequently swollen to form a 'plateau.'" I have found but few specimens in Oklahoma which show this character and all which I have seen came from the northwestern or southwestern part of the state and some of these within fifteen miles of the Kansas line. Since I have collected many specimens in all parts of the state, it seems probable that this represents a real difference in these toads in Kansas and Oklahoma. Again, he states, "belly usually immaculate or with a single median dark breast spot." Most specimens in Oklahoma fit this description but it is not at all uncommon to find considerable spotting on the venter, particularly on old females. I have frequently found specimens with a series of spots around the ventral insertions of the arms and others with minor spotting in various degrees from the anterior half of the belly to the lower jaw. Pectoral spots are common, though not universally present on specimens from Oklahoma. Frequently, a single large or small breast spot occurs but this often is broken up into two, three, or a cluster of smaller spots. They occur more often on females than on males and are sometimes to be seen on very young toads. I have seen them on individuals only 27 mm. in length.

Dorsal variations are also common. Some specimens are almost black; others are so light as to suggest tan. The two extremes are, however, rare. The spots on the back vary from two (seen in one specimen only) to fifty or more. In general, the fewer the spots the larger they are individually, although there are some exceptions to this. In some individuals, the spots tend to be

arranged in pairs much as described in detail for *Bufo fowleri* Hinckley by Dickenson (1913).

Several descriptions of *B. w. woodhousii* mention the dark throat of the male. However, apparently few have noticed that this secondary sex character is more conspicuous during times of breeding, although the phenomenon is well known among Anura. During March, April, and May in central Oklahoma, a glance at the throat is sufficient to distinguish the sexes; later in the summer, the male's throat often becomes almost as light as that of a female, though it never is quite so when a thorough examination is made.

The "protesting" note uttered by the male when handled is distinctive. It is a low, semi-trilled, "fussing" sound which may be kept up for long periods or given intermittently. I have found by experiment that I can invariably distinguish a male of this species from all other toads known to me by this sound alone. This was done by picking up individuals at random in the dark. I have frequently confounded *B. cognatus* and *B. compactilis* by this method and I have sometimes missed *B. a. americanus* but I have never failed to distinguish *B. w. woodhousii* from all others. As with most toads, females do not usually protest when handled. However, some small females will give a sort of surprised "peep" when caught suddenly and thereafter remain silent. I have never known an old female to do even this.

The daily cycle of activities of *B. w. woodhousii* varies somewhat with the age of individuals. As the young toads come from pools after metamorphosis, they take advantage of the moist area surrounding the pool. Even in very hot dry weather, many of them remain active throughout the day and seek shelter only under exceptional circumstances. In May, 1938, for example, tiny toads of this species were abundant on moist sandy soil on the flood plain of the Canadian River every day for two weeks following their metamorphosis in spite of warm sunshine. They avoided adjacent dry sand dunes, however. On another occasion, in a similar situation on the Cimarron River in mid-July, on an afternoon when the temperature was 102° F., only one tiny toad was active, and this in the shade of a bridge; all others had sought shelter under driftwood or clods of clay. At still another time, in modified mixed-prairie, many recently emerged young were found in short vegetation on just barely moist ground on a warm bright day; none inhabited the drier, bare areas and none were found in adjacent tall grass. Ten days later (with maximum temperature above 90° F. on each day and with no rain), only two individuals were taken in the short vegetation, many were in the tall grass (apparently seeking shade); one was hiding under a ledge, and the remainder (at least seventy-five and probably more) were congregated on the moist soil surrounding a rapidly drying pool in a draw nearby. Eleven days from this time (with maximum temperatures 95° to 108° F. and no rain), hundreds of tiny toads were found farther up this draw on moist soil and some of the larger ones were in the tall grass adjacent to it in late afternoon.

Even though tending, thus, to be diurnal, the young toads are also often nocturnal as well. On several occasions, I have found them at night, usually on moist soil but sometimes even on very dry and dusty gravel roads. I have

not determined whether the same individuals are active during both day and night but I would expect this to be the case.

When from one to two months of age (i.e., after metamorphosis), the small toads become less and less diurnal and at about two months become largely nocturnal like the adults.

From considerable experience, I have a definite impression that the adults of these toads tend to emerge to feed later at night as they increase in age. In the early evening, one seems to find more of the smaller toads than of large ones, as the hours pass, larger individuals are found in greater numbers, till after one or two A.M. the toads about streetlights are mostly old females with an occasional male or juvenile among them. There are many exceptions to this generalization, however, and this is especially true in moist weather.

I have a similar impression that males are more susceptible to dryness than are females. For example, at several times while collecting at night I have taken many females and few or no males in regions where no recent rain had come, but upon entering an area where a shower had recently fallen about as many males as females were taken. In one such case, I drove in an automobile from a dry area, through a moist area, to another dry area on the other side. Many more males were found in the middle one of these regions than in either of the others. Not only was this true but also the proportion of males was greater in the moist region.

Bufo w. woodhousii is a very alert, active toad, much more so than *B. cognatus* of the same region. In captivity, they are continuously active in their attempts to escape but they soon learn that this is impossible when in a covered container or in one too deep for them to jump out. When encountered on a road at night, they often start immediately for the vegetation by the roadside to hide. Even the recently metamorphosed young are alert to danger, very active, and difficult to catch as compared to *B. cognatus* of the same sizes.

Breeding Activities

Bufo cognatus breeds only after rain and, till recently, I had supposed that this was also true of *B. w. woodhousii* (Bragg, 1940). Off and on for several years, reports have come to me of toads calling during dry times but all such reports remained unconfirmed until the spring of 1939.

On March 23, Dr. J. Teague Self reported that he had heard a large congress of toads on the Canadian River flood plain the previous evening. That night, I visited the area designated at 8:15. One of the largest congresses of *B. w. woodhousii* in my experience was found in the shallow water held by a dam of sand thrown across a slough at the edge of the flood plain. *Pseudacris streckeni*, *Pseudacris* sp., and *Rana sphenocephala* were also calling here in some numbers. No females were seen at this time.

The most recent rain had been 0.02 in., on March 10 (two weeks previously), according to the records of the weather station at the University of Oklahoma, about two miles distant. The total precipitation for March prior to this date was only 0.49 in. and for the month previous, 0.07 in.

Two days after this congress was found (i.e., on March 25), 0.59 in. of rain came. Several clutches of eggs were produced that evening and others on succeeding nights. On April 1, unmistakable evidence of ten clutches of eggs were found here, some just hatching and others recently hatched.

These observations proved that males of *B. w. woodhousii* may become sexually active in quite dry weather and seek females, provided they can find water from which to call. They do not indicate, however, whether females will join the males and produce eggs under these conditions.

Evidence on this point was soon obtained. April was dry throughout central Oklahoma, only 0.21 in. being recorded in Norman. On the 28th Dr. Roy W. Jones of Edmond reported a clutch of eggs of *B. w. woodhousii* in an artificial gold-fish pool in a garden there. He said that there had been no recent rain. On May 4, thousands of recently hatched tadpoles of *B. w. woodhousii* were found in a similar pool in Norman. There had been no precipitation since April 27, and then only 0.02 in. and the last rain of consequence had been over a month previously, 1.03 in. on March 29.

Several bits of circumstantial evidence (such as the finding of metamorphosing young during June and July in several localities), when added to the conclusive evidence just given, indicate beyond doubt that rain is not always a necessary precursor to the breeding activities of this toad. But even though this is true, the great bulk of breeding does occur after spring and summer rains, provided the temperature is not too low. As with *B. cognatus*, so with the Rocky Mountain toad, males call vigorously after rains of one inch or more at any time, at least from late March to mid-August and most eggs are produced under these conditions. The latest seasonal record of calling males which I have is August 9, 1939, in southwestern Oklahoma.

The breeding sites of this toad are quite varied in character. They include flooded ditches, flooded fields, pools formed in gravel-pits, fish-pools in gardens, sloughs along the larger streams, cattle-tanks[2] in pastures, and the shallower portions of the littoral zone of small, relatively permanent artificial lakes. Males also sometimes enter medium sized buffalo wallows and clasp females of *B. cognatus* (one observation only) but females of *B. w. woodhousii* apparently avoid these for I have never found one in such a place and know of no eggs or young being produced in a buffalo wallow.

In comparing the breeding sites of *B. w. woodhousii* and *B. cognatus*, it is of considerable interest to note that they seldom coincide in and about Norman, Oklahoma. A large congress of the latter species may be gathered about

2 Throughout Oklahoma, water for cattle is provided in pastures by the construction of earthen dams across areas of natural drainage, thus catching the run-off whenever rains come. The resulting pools are locally called "tanks." Some are quite extensive, one-half acre or more, but others are small. In most of them the water is very muddy. The pool is transitory or permanent depending upon size, depth, the rate of evaporation, and the distribution of rainfall within any one season. Tanks have a rich and extensive fauna and flora, particularly of invertebrates, amphibians, and algae, which would well repay detailed investigation by anyone interested.

buffalo wallows within fifty or a hundred feet of a cattle-tank where *B. w. woodhousii* are calling without the two species mixing.[3]

The only constant difference which I can find between sites chosen by the two species is the roiliness of the water. For *B. cognatus*, the water must be fairly clear but *B. w. woodhousii* avoids clear water if roily water is present. There is only one region about Norman where the two species breed extensively in the same water. This is a low field, bordered by a deep ditch, located just southeast of the polo-field of the University of Oklahoma, at the southern edge of the city.. (For a picture of this area, see Bragg, 1940, Fig. 5) Here, following spring rains, the two species (as well as several other Anura) intermingle freely, although *B. w. woodhousii* uses both ditch and the field whereas *B. cognatus* is always restricted to the shallower water of the latter. It was here that the crossed pair was taken which was reported upon earlier (Bragg, 1939a).

While calling, males sit in the shallow water, usually at the edge of the pool but sometimes farther out. More rarely, they call from the bank, almost invariably facing the pool. They are much more alert and shy than sexually active males of *B. cognatus* and often plunge into the pool to hide on the bottom after the manner of frogs, when approached, even late at night.

The usual call of the species is well known, a short, more or less trilled "baa" which may be heard and recognized from considerable distances. It is not generally known, however, that males of *Bufo w. woodhousii* sometimes give voice to another, althogether different type of call. This consists of a single short note, suddenly and almost explosively given. It may be described as closely approximating the word "whew" pronounced with rather high pitch, drawn out rather long, and having a slightly weird, rising inflection at the close.

I have heard this call in breeding congresses of Anura at several times in widely scattered portions of Oklahoma and for a long time was puzzled by it. In each case, but one or two individuals were heard and the typical cry of *B. w. woodhousii* was more numerous. Eventually, a male was captured just after he was seen to call in this manner and it proved to be a large individual of *B. w. woodhousii*. Inasmuch as each species of frog or toad usually has a very distinctive sexual call, the finding that *B. w. woodhousii* has two of these is of some interest.

The usual congress of males of this species is small although, especially after heavy rains, congresses of several hundreds may occur. It is more common to hear one, two, or numbers up to a dozen or so about any one pool on a given night. I find no evidence of the building up of huge congresses as in *B. cognatus* by the reactions of the males to the calls of one another. Instead, each male acts individualistically and calls or ceases to call with little or no regard to others about him. Because of this individualistic tendency on the part of *B. w. woodhousii*, there is little tendency for the calls in a congress

[3] I am indebted to Mr. Albert H. Trowbridge of the U. S. Biological survey for first calling this to my attention in 1935. Since that time I have confirmed the observation at several different times and places.

to be localized in one place in a pool, a phenomenon which is characteristic of several species of toads, e.g., *Bufo cognatus, Bufo compactilis,* and *Bufo insidior.* I had a fine opportunity to observe this difference between *B. w. woodhousii* and the other species mentioned one night in the summer of 1939. After a rain in southwestern Oklahoma, Dr. Charles C. Smith and I found the four species breeding in numbers in an extensively flooded area at Duke, Jackson County, Oklahoma. This was near two A.M. on the morning of August 9. The *B. insidior* were all congregated near one end of the pool. Along one side, fifteen or twenty *B. cognatus* were calling. Along the other side hundreds of *B. compactilis* were swimming about excitedly and clasping one another or calling all along the bank. Because of the large numbers of *B. compactilis* present, a few individuals were over into the edge of the *insidior* section of the pool, but except for this, the whole flooded area could be strictly divided into separate areas, one occupied by each species. *B. w. woodhousii,* however, had no such section of the pool but males were calling all around it with no regard for each other or for the members of the other species about them so far as we could determine.

As is common with toads, males of *B. w. woodhousii* usually exceed females in numbers in breeding pools and they come to the water earlier in the evening than females. If one may judge by the ratio of males to females found during nights of feeding, females actually exceed males in numbers in any given population. If this be true, then it is likely that not all females breed each year—indeed it would seem that only a small fraction of them do so even when opportunity is afforded in the form of plenty of water and of many clamoring males. Further evidence of this has been found, for several large females which still retained eggs have been collected in late July in a region where some members of the species bred successfully earlier in the season.

B. w. woodhousii, like the American toad of the East (Miller, 1909), often produces several clutches of eggs very close together in a pool when there is no apparent reason for it. On one occasion, for example, I found eleven clutches within an area of about fifty square feet whereas none whatever could be found in the remainder of the flooded area which was about an acre in extent and nearly all quite uniform as to type. There had been numerous males approximately equally distributed about the pool the previous night. That this observation was not likely a matter of chance is indicated by the fact that later in the same season the phenomenon was observed again in this same flooded area, but the eggs were congregated at this time in another part of the pool. It is difficult to correlate these facts with the individualistic actions of the males noted earlier. For this reason, it seems likely that they will be explained by some reactions of the females which at present are not understood.

The eggs have been described and figured by Smith (1934) and the larvae by Youngstrom and Smith (1936) and by Johnson (1939). Since my observations confirm the work of these authors in all essential particulars, it is unnecessary to dwell upon these phases of the life history. The egg—complement is large (more than 25,000 in one reported by Smith, 1934). Eggs are usually but not always laid in shallow water, usually close to the shore. Tad-

poles hatch within three days (Youngstrom and Smith, 1936). The larval period is short. Youngstrom and Smith give thirty-five days as its minimum length and this compares favorably with the thirty-four days of larval life which I observed on the flood plain of the Canadian River in 1938.

The Process of Hatching

The process of hatching of anuran larvae has received scant attention (See Bragg, 1940b). Noble (1926) reviewed the literature to the date of his paper and presented histological evidence of the presence of a frontal gland on the head of the larva which is supposed to produce a substance that dissolves the jelly. The mechanics of the process in *B. cognatus* were described in the first paper in this series (Bragg, 1940) but I know of no description of it in *B. w. woodhousii*. Since the details of the process in the latter differ remarkably from those in the former, it seems advisable to present the findings in some detail. The description is based upon forty observations, all from the same clutch of eggs, developed in the laboratory at temperatures which had ranged from 30° to 33° C. since the eggs were laid by captive toads. The study was made with the aid of a low-powered binocular microscope.

During cleavage, the embryo is surrounded by two membranes, (1) a very thin one closely applied to the embryo and (2) a portion of the long gelatinous tube characteristic of most kinds of toad's eggs. There is no inner gelatinous capsule as in *B. cognatus* and the outer tube does not show laminations when stained with Schneider's aceto-carmine (Bragg, 1937).

Development progresses with little increase in size till after the neural tube closes—in fact, the increase is not nearly so great as that recently determined for *B. cognatus* (Bragg, 1939b). Just after elongation of the body begins, as the body axis is being laid down, liquid begins to accumulate about the embryonic body, forcing the thin membrane away from the body of the animal. From this time onward. the organism appears to lie in a bubble the walls of which are distended and under considerable hydrostatic pressure.

In the meantime, the gelatinous tube softens materially and often becomes more transparent than formerly. Eventually, rather large and irregularly shaped holes appear in the tube, one opposite each bubble. The embryo becomes externally ciliated at about this time or slightly before and the action of the cilia may rotate the embryo slightly from time to time.

While the embryos are still small, the bubbles begin to work gradually through these openings and come to lie free in the outside medium. Just how this is accomplished could not be determined with certainty but it seems probable that the increasing size of each bubble, due to the gradual accumulation of liquid within it, causes the pressure which forces the bubbles through the openings previously formed in the tube.

Some hours later, the embryo within each bubble begins a slow rotation. For the next hour or so, the rotation continues at a rate of about 1.75 complete turns per minute, although occasionally an embryo may slow down somewhat or even cease turning altogether momentarily. The head of the embryo is closely applied to the wall of the bubble during this time but the posterior end

may not be; and each embryo rotates with the dorsal surface going before, usually to the left. Whenever in its growth the embryo becomes longer than the diameter of the bubble in which it lies, the head becomes bent to one side.

After a rotation of about one hour, varying a little either way, the membrane breaks quite suddenly, usually but not invariably in the region of the head. Most of the enclosed liquid is released and the wrinkled membrane can be seen over most of the embryo. The embryo continues to rotate feebly for some time after this. Meanwhile the wrinkles of the enclosing membrane become more difficult to see, till eventually they disappear entirely and the larva falls gently to the bottom of the container.

The adhesive organ is functional at this time and often the larva catches upon the jelly of an egg-string on the way down. Failing this, its movement along the bottom, caused by the beat of external cilia, eventually carries it to some object to which it adheres.

As noted by Youngstrom and Smith (1936), the tadpole hatches in a premotile condition, that is to say, no muscular movements occur prior to or during hatching.

The exact observations on one embryo are summarized below:

8:00 P.M.	Rotation just starting.
8:53	Membrane broke.
9:00	Wrinkled membrane pressed against embryo.
9:15	Rotation continuing with pauses; embryo sliding about inside the membrane; membrane narrower.
9:45	No visible change.
10:00	Head of embryo straightened; little membrane visible.
10:30	No membrane visible except a few strands on posterior end of embryo; rotation stopped.
10:32	Larva moving along bottom of container.

There is still one thing which is not clear about the process of hatching—the cause of the appearance of the openings in the outer, gelatinous tube. It does not seem likely that a secretion of the embryo would pass osmotically through the wall of the inner membrane and dissolve the jelly, yet how else is one to explain the positions of the openings, one opposite each embryo? The facts that the inner membrane appears to become thinner during the rotation of the embryo and that it gradually disappears slowly as though dissolved, strongly suggest a secretion of the embryo such as indicated by Noble (1926) for some other species; but if such is the case, why does the *outer* membrane give way first? Is it possible that in *B. w. woodhousii* two secretions are involved, the one passing through the inner membrane without effect upon it, the other produced later during the rotation of the embryo and dissolving the inner membrane after the bubbles have been released? The answers to such questions must await experimental answers.

One of the most interesting things about these observations of the embryos of *B. w. woodhousii* is that two so closely related species as this and *B. cognatus* can differ so radically in a comparatively simple process. Although I

have always maintained that generalizations about several species from the study of one or a few are dangerous to scientific accuracy, I must confess to great surprise when I first saw a larva of *B. w. woodhousii* hatch.

In *B. cognatus*, the rotation of the embryo appears to be quite incidental to the process of hatching—in *B. w. woodhousii*, it seems quite essential to it. In the Great Plains toad, the emergence of the larva from the membranes is so sudden as to be almost explosive—in *B. w. woodhousii*, it is so gradual as to seem hardly to have a definite beginning and end. In fact, the details of the process differ so radically in the two species as to make one wonder at so much evolutionary divergence from the common type presumably present in the ancestral toad.

Factors Limiting Numbers

Little is known about the factors tending to limit the numbers of toads except for the estimates and observations of Miller (1909) on the American toad and the few observations reported previously for *B. cognatus* (Bragg, 1940).

The known predators of *B. w. woodhousii* in Oklahoma are the following: the hog-nose snakes (*Heterodon* spp.), black-snakes (*Elaphe* spp.), bull-snakes (*Pituophis sayi*), bull-frogs (*Rana catesbeiana*), and hawks (one observation by Dr. Charles C. Smith). It seems probable that garter-snakes (*Thamnophis* spp.) and water-snakes (*Natrix* spp.) are also predators although I do not know them to be for a certainty. Along the Cimarron River particularly, and in other parts of the state, many hundreds of the young of this species are caught and used as fish-bait each summer. Here they are known locally as "sand toads," probably because they are collected from beneath drift-wood, partially buried in the sand of the flood-plain.

Winter-killing of toads in Oklahoma appears to be negligible. A few die from becoming trapped in holes. The automobile kills thousands each year, especially after rains, but it is doubtful if as many are killed in this manner as of the Great Plains toad because of the greater alertness of *B. w. woodhousii*.

The ecological factors affecting tadpoles of this toad have not been studied. *Scaphiopus bombifrons* and *S. couchii* often breed in the same pools and at the same time as *B. w. woodhousii*, the former in central Oklahoma, the latter in the south and southwest. It is probable that the large predaceous tadpoles of first mentioned spadefoot catch the larvae of the Rocky Mountain toad as they are known to do to *B. cognatus*. Whether the smaller carnivorous tadpoles of *S. couchii* do so is problematical. Predaceous beetles and bugs occur abundantly in breeding pools and presumably also take their tolls, and salamanders and fishes are probable predators in some of the larger tanks and small artificial lakes.

The breeding sites utilized by *B. w. woodhousii* insure that at least some young will be produced each year in any given region. In one pool observed,

B. w. woodhousii has produced eggs each year since 1934. In 1938 hundreds and probably thousands of young emerged but in 1939, although eggs were laid at three different periods during the spring and early summer, the pool dried up each time before any of them could complete the aquatic phase of existence. But in several other pools during the latter year young toads were found emerging in June and July.

Another factor in the successful production of at least some young during practically every year is the habit of the adults, previously mentioned, of not all breeding at the same time, even under the most favorable of conditions. A few adults breed in very dry spring seasons when there is no rain; a larger number breed following the first heavy rains in spring or summer; but some breed after rains in July or August even when there has apparently been every opportunity to do so earlier. If rain does not come in late summer, some individuals do not breed at all during a given season. It is obvious that this habit of "staggering" the breeding activities is valuable in a climate as dry as that of Oklahoma and it is probable that it is one of the main reasons for the wide distribution of the species in the state.

Metamorphosis and Growth of Young Toads

Metamorphosis begins at a tadpole length of about 30 mm. (average of 47 was 29.49 mm.). After about a week during which the hind limb buds enlarge rapidly, a very quick transformation of the whole body sets in through which a tiny toad is formed from the tadpole in about three days. At emergence from the water, each young toad usually measures between 12 and 13 mm. although some are slightly smaller or larger than this. The average length of 47 emerging toads was 12.71 mm.

The young toads are distinctive in appearance. Their color dorsally is a grayish brown with a varying number of dark spots which are the forerunners of the spots on the backs of adults. During metamorphosis, the back also becomes peppered with small red dots similar to those on *B. cognatus* of the same age. The ventral surface is of clear white, except that on some a dark pectoral spot appears very early.

They begin feeding immediately upon small insects, small spiders, and mites and the rate of growth is very rapid. For example, during the month from June 26 to July 26, 1939, collections of young toads in the area adjoining the pool from which they had come were made at approximately ten-day intervals and their lengths measured in mm. During the month, the average total increase in length was 9.3 mm., which is the equivalent of 0.3 mm. per day. Expressed differently, these toads lengthened at the rate of 3.23% per day on the average, though at the end of the period they varied more in size individually than at the beginning. If this rate could be continued throughout the first summer, the average first-season toad in the fall should be about half grown. That this is actually the case was shown in the autumn of 1938. Twenty-one young toads, known to be between four and five months of age,

collected in early October, varied from 43.0 to 65.0, about an average length of 53.36 mm. From the above it is evident that the general pattern of growth in young *B. w. woodhousii* is the same as in *B. cognatus*.

Summary

Bufo woodhousii woodhousii (Girard) inhabits the central plains and mountains from Nebraska to Texas and from Arkansas to southwestern California. In Oklahoma, it inhabits all areas possible to a toad in all parts of the state except the northeast and southeast. It is especially abundant in sandy areas and in lowlying bottom lands and it is the only toad found on the sandy flood plains of most, if not all, of the larger streams. It is the common toad under street-lights and about gardens and lawns but is not so numerous in the eastern third of Oklahoma as elsewhere in the state. It is one of the most active and versatile of toads.

Not much is known about the factors which tend to limit the numbers of this species. The larvae are probably preyed upon by tadpoles of Scaphiopus and by aquatic insects and possibly by other carnivorous animals. The known predators of adults include snakes (of several species), bull-frogs, and hawks. Many are killed by automobiles.

These toads breed in a great variety of places (cattle-tanks, ditches, flooded fields, back-washes of streams, artificial fish-pools, edges of small semipermanent artificial lakes, and sloughs on the flood plains of rivers). They are not known to use buffalo wallows and their general versatility and adaptability to conditions make this hard to explain. They seem to prefer shallow water for breeding but have been known to produce eggs in water at least three feet deep. They seem to prefer muddy water but will use clear water at times. Within any one season, the breeding activities are staggered—that is, not all individuals breed at the same time even under favorable conditions. They are not dependent upon rain for breeding although most breeding activity does occur after rains in spring or summer. Congresses of this species are usually small and each male acts more or less individualistically, calling or not according to some inner urge, quite unlike *B. cognatus*.

Metamorphosis occurs at a total length of about 30 mm. after a tadpole period of from 34 to 45 days, dependent upon both temperature and food supply. The food of the larvae is Algae and organic debris of either plant or animal origin. The young toads are spotted dorsally in two colors on a grayish brown background. The larger spots are dark colored and of medium size; the smaller are tiny and red, like the peppering on young *B. cognatus*. The young toads are active and alert. They feed upon small insects and arachnids and may grow at a rate of 0.3 mm. (i.e., about 3% increase) a day. Some become half grown during the first summer and, in this respect, resemble *B. cognatus*.

The main differences between the habits and habitat of *B. w. woodhousii* and *B. cognatus* may be summarized as follows:

B. w. woodhousii

1. General habitat unrestricted; most common in sandy areas.
2. Common about human habitations and street-lights.
3. Breeds in many places, often in muddy water; never observed in buffalo wallows.
4. Usually breeds in shallow water but may use deep water.
5. Breeding in any one season is staggered, regardless of conditions.
6. Most breeding after rain but some breeding occurs irrespective of rain.
7. Breeds usually in small congresses; calls of males with little effect on each other.

B. cognatus

1. General habitat quite restricted; found mostly in mixed prairie.
2. Uncommon, but occurs, about human habitations and street-lights.
3. Breeds only in relatively clear water, most commonly in buffalo wallows and flooded fields.
4. Breeds only in shallow water.
5. Breeding not staggered if sufficient rain comes.
7. Breeds usually in large congresses built up by the reactions of males to one another's calls.

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Observations on the Ecology and Natural History of Anura. III.

The Ecological Distribution of Anura of Cleveland County, Oklahoma, Including Notes on the Habits of Several Species[1]

Arthur N. Bragg

For several years, observations on the distribution and habits of the frogs and toads in Cleveland County, Oklahoma, have been made, at first more or less incidental to the study of toads (Bragg, 1936, 1937, 1937a, 1939, 1940, 1940a) but later extended to include all species present. During the spring of 1938 and the spring and summer of 1939, extensive observations have been made and specimens collected in all parts of the county at all hours of the day and night.[2] It is on these, supplemented by many notes taken earlier, that the present contribution is based.

The paper is intended primarily as a study of the different species of Anura present in the county and their distribution and abundance in the major ecological communities which occur there. Distributional records are, therefore, mentioned only incidentally. Nevertheless an attempt has been made to include all forms reported from the area under consideration to the end that the paper may serve as a summary of our knowledge of the anuran fauna in this limited section of central Oklahoma. Most of the species mentioned have also been collected across county-lines in comparable habitats, so that the paper may almost serve as a summary for central Oklahoma in general.

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Ecological Divisions of Cleveland County

Cleveland County, Oklahoma, is an approximately triangular area of 555 sq. mi., located in the central portion of the state (Fig. 1). It is bounded on the north by Oklahoma County; on the east by Pottawatomie County; and on the south and west by McClain County across the extensive sandy flood-plain

1 Contributions from the Zoological Laboratory of the University of Oklahoma, No. 208.

2 Transportation for collecting and making observations was made possible by a grant from the Faculty Research Fund of the University of Oklahoma.

of the Canadian River. In the extreme northwestern portion, it also touches Canadian County, north of the Canadian River.

About half of the county to the east is hilly and sandy. Here, three ecologically important habitats exist: (1) an oak-hickory complex, taking the form of savannah on most slopes but in some regions becoming typical woodland; (2) "islands" of grassland in valleys which have been cleared for agricultural purposes or on exposed hilltops where climatic or edaphic factors favor the growth of grasses rather than of trees; and (3) heavily wooded bottom-lands in the valleys of the larger streams, particularly of Little River and its main tributaries which drain most of the northern and eastern parts of the county (See Brown (1931) for a more extended account of the Oak-Hickory Association in Cleveland County.)

The western portion of the county is typical mixed-grass prairie, dominated by *Andropogon* and *Sporobolus* along its eastern edge, by *Andropogon* and *Aristida* in its central portion, and by *Andropogon* and *Panicum* on or near the flood-plain of the Canadian River. The presence of the genus *Aristida* is explained mostly by overgrazing and other disturbances.

Two important subdivisions of this prairie are recognized as habitats for Anura: (1) the higher portions of the rolling grassland and (2) the lower areas along creek-beds or along the larger gullies caused by erosion where trees (particularly elms) get a foothold in response to slightly moister conditions. Such regions are hereafter called ravines. For a discussion of essentially similar regions in McClain County nearby, see Carpenter (1937).

The flood-plain of the Canadian River in Cleveland County has been studied extensively by Hefley (1937). The vegetation includes (1) a band of woodland (often cottonwood-parkland) on the higher levels facing the prairie; (2) a tangle of willows, tamarisk, and young cottonwoods along the sloughs and sometimes extending on to sand-dunes thrown up by the prevailing southwesterly winds of summer; and (3) bare sand or sand with sparse vegetation (cockle-burs, grasses, sedges, etc.) on the lower levels of the plain.

Breeding sites for Anura in the county are quite variable in character. They include (1) back-washes of the larger streams, (2) pools in creeks, (3) artificial ponds and lakes, (4) flooded ditches, (5) flooded fields, (6) buffalo-wallows in prairie-pastures, (7) pools in pastures known as cattle-tanks (or simply, tanks), and (8) sloughs along the edge of the flood-plain of the Canadian River, produced principally by creeks entering the plain (whose riverward course has been obstructed by drifted sand piled up into dunes during protracted periods of dry weather).

In all but the largest of these sites, water remains only a short time after rains, although the puddling of the underlying clay-soil in buffalo-wallows and some prairie tanks by the stomping of cattle tends to limit underground runoff (Barkley and Smith, 1934). In most of these breeding-sites, the water is very muddy, especially after heavy rains when most of the breeding activities of all species occur. However, most buffalo-wallows, the more grassy pools in flooded fields, and the sloughs along the river usually are fairly clear when Anura breed. Tanks and ditches are almost invariably heavily laden with

suspended red clay (an effect of erosion), some in simple suspension, some in colloidial solution so that it does not easily settle out even when undisturbed for long periods.

Buffalo wallows have not been found and apparently do not occur in the Oak-Hickory association. Most amphibian breeding here occurs in muddy ditches, tanks, flooded fields, and the backwashes of streams. In the prairie, breeding of most species is in temporary pools of all sorts, although some species have been found to be restricted to certain types of sites (Bragg, 1940, 1940a). On the flood-plain of the Canadian River, the sloughs are utilized in the breeding of all species present there, but some portions of them seem to be more favorable than others for certain species. Pools in creeks are used rarely by *Acris crepitans* and by *Rana sphenocephala* but I have never found evidence of other species using them for breeding.

The Anuran Species of Cleveland County

Fourteen species or subspecies of Anura have been reported from Cleveland County or are here mentioned for the first time. Of these, I have succeeded in collecting twelve, usually in some numbers and on many occasions. In passing, perhaps it is well to mention that I have heard another unreported species, probably of *Pseudacris*, in many places in the county but have never succeeded in securing a specimen. Representatives of all forms collected will be found in the University of Oklahoma Museum of Zoology.

A list of these Anura, together with notes on their habits and ecological distribution, follows:

1. *Bufo americanus americanus* (Holbrook)

The American toad is widely distributed in the Oak-Hickory Association in the eastern part of the county. It has never been found elsewhere. During May-June, 1939, it bred successfully in the edge of the woods within one-half mile of the eastern edge of the prairie, four miles directly east of Noramn, and this point marks the westernmost limit of its range, so far as now known, in Oklahoma. Males were heard here early in May and the young transforming toads were collected in early June at the edge of a tank in a pasture. From this point eastward, *B. a. americanus* is fairly abundant in the woodland, at least to central Pottawatomie County where males were heard calling in late June after a rain.

It breeds in muddy tanks and flooded ditches throughout this area. Eggs have been found as early as May 9. More males call after rain but eggs may be produced irrespective of rain if there is sufficient water in the pools. The tadpole period in this habitat is much abbreviated. Instead of the usual 50-65 days (Wright and Wright, 1933), exactly thirty days elapsed from egg to metamorphosis in two different pools and also in a laboratory culture in 1939. The heightened rate of development may be due to the effect of high temperatures alone or it may be correlated with the small size of the adults as explained below.

The eggs, egg-membranes, and larvae of these toads conform to the usual

descriptions for *B. a. americanus*, but the adults are somewhat exceptional, especially as to size. The extremes in length of the members of this subspecies are usually as follows (Wright and Wright, 1933): males, 51-74 mm.; females, 56-82 mm. Three series of these toads averaged as follows: 15 males, 56.8; 12 males, 57.0; 25 males (Table 1), 56.92 mm. Only one female has been found, an adult collected while laying eggs. She measured 72 mm.

It will be noted that most of these measurements are within the reported size-range for the subspecies. What is interesting is that of more than a hundred collected or seen, all were small. Since all of these specimens except one were taken while they called about breeding-pools, there is no question as to their being adults. Inasmuch as specimens of normal size are known from farther east and south in Oklahoma, I interpret this as a clear case of dwarfing at the western limits of the range.

In order that these somewhat exceptional toads may be compared with others from other regions, I include below a description of one of them which is taken as typical of all. In addition, Table 1 gives proportional measurements upon a series of twenty-five.

Sex, male: length, tip of the snout to the anterior border of the vent, 59.0 mm.; color, dorsally a yellowish brown, tending to a reddish brown anteriorly. A series of reddish-brown warts, arranged not quite in pairs, each surrounding and often partly covering black spots which are in turn surrounded by cinnamon-colored areas. Numerous other smaller warts, irregularly scattered, mostly reddish-brown in color, and without black rims. An occasional small black spot or dot, rimmed with cinnamon, elsewhere on the back. A mid-dorsal stripe, whitish in color, extends from about midway between the parotoids to two-thirds the way down the back, widest anteriorly, becoming narrower and less conspicuous posteriorly and with faint indications of it all the way down. Dorsal surface of the thighs with vermiculations of black and with numerous spinous warts of small size. Shanks with larger spinous warts, each with a single spine. Cranial crests conspicuous from the anterior level of the eyes, slightly divergent to the postorbital crests, a spur running mesiad from this point. Postorbital crest and cranial crest make right angle posterior to the eye on the left, not quite so on the right. Postorbital crests dipping ventrolateral between the eyes and the anterior borders of the tympana, each sending a spur backward to the outer anterior border of the parotoid. Paratoids long, just less than one-third of the length of the body proper; somewhat kidney-shaped and nearest together in the middle. Eyes protuberant, with small warts on the upper eyelid. Tympanum smaller by about one millimeter than the eye, bordered posteriorly by a slight fold of skin. Angle of the mouth slightly posterior to the posterior edge of the tympanum (by about one millimeter). A group of spinous warts between the tympanum and the foreleg. Nostrils close together. Lateral surface colored like the dorsum above, but with black vermiculations in its central and ventral portions, the black extending irregularly upward at the groin and continuing along the posterior surface of the thigh to the vent. Two small reddish warts just craniad of the cloacal opening on the dorsum. Ventral surface granular; background generally light

(just off white), but with rather large black irregularly shaped spots from the posterior of the insertions of the arms to half way down the venter. A large elongate black breast-spot, extending from just below the vocal pouch to the posterior level of the insertion of the arms. Throat-pouch dusky (not truly black); anterior to this the throat has "watery-orange" color which extends also downward along the ventral surface of the lower jaw. Some of this same color on the ventrum of the thighs and on the posterior portion of the belly. Upper jaw with a distinct notch in front, the lower with a corresponding protuberance. Iris distinctly golden but with fine black vermiculations. Two metatarsal tubercles; the outer rounded, the inner larger and with edge not heavily cornified at the time of description.

Other toads in this series vary much in coloration from the specimen described. One is almost black; another almost yellow, it is so light. The predominant color, however, is a reddish-brown, even after the animals have been confined for some days in a dark, moist container. This color closely resembles the soil of the habitat.

The heads of these toads seem rather small for the bodies. The line along the lateral edge of the body and head is not a gentle curve. Instead, it becomes almost straight at the tympanum and then curves in a different arc anteriorly to the front of the jaw.

The single female taken was comparable to the males, except for the expected differences in secondary sex characters (i.e., wider waist, larger size, and the lack of dark color on the throat).

The attitude of these toads is one of alertness. They are forever attempting to escape when in captivity. About the breeding-pools at night, their behavior differs at different times. Often they will continue to sing even when a flash-light is played upon them. Sometimes, however, they will leave the pool completely and hop away. In the latter case, they usually do not return for some time to the pool, even after all is quiet.

The protesting note of the male is a pleasing "peep" or short trill, the latter more often given by use of the vocal sac when first caught and handled roughly. The breeding call varies little if at all from the typical high-pitched long trill that is so familiar to all who know the toads. As might be expected, the single female collected remained silent when caught.

These dwarf toads have been seen only about pools and only during their breeding activities in April, May and June, although searched for at other times. They are, therefore, secretive like the American toads of Kansas observed by Smith (1934).

2. *Bufo cognatus* Say

The Great Plains toad is very abundant in the prairie, where it is the dominant toad (Bragg, 1940). It breeds only after rain in temporary water which is fairly clear. It is also found in limited numbers on the larger of the prairie islands in the Oak—Hickory Association but it is not in the savannah, woodland, nor bottomlands. It has been found but once (a single individual) on the flood-plain of the Canadian River although it follows the grassland in

numbers to the very edge of the cottonwood parkland bordering the plain. In the eastern part of the county, it breeds only in flooded fields where the water is clear.

3. *Bufo woodhousii woodhousii* (Girard)

The habits and distribution of the Rocky Mountain toad in Oklahoma have recently been studied in detail (Bragg, 1940a). In Cleveland County, it is universally distributed more or less irrespective of ecological microhabitats. It is more numerous in the Oak—Hickory Association than the American toad, it is common but not so abundant as *B. cognatus* in the prairie, and it is the only toad found on the flood-plain of the Canadian River, where it is very abundant. It breeds in clear or muddy water, either temporary or permanent, but usually avoids the breeding sites chosen by *B. cognatus*. It is not known to use buffalo wallows, which are the natural breeding sites of the latter species. When pools of both muddy and clear water are present together, *B. w. woodhousii* almost invariably uses the former exclusively for breeding activities; but when only clear water is available, this is used readily by some individuals. Most eggs are laid in shallow water but young toads of this species have been seen emerging from water at least three feet in depth. Not all individuals breed in any one year; in fact, the breeding activities are "staggered" through each spring and summer in such a manner as to take advantage of available pools whenever they are formed. Most breeding occurs after rain, but some individuals breed each year whether rains come or not, provided, of course, that the males can find water from which to call.

B. w. woodhousii is the common toad about streetlights, dwellings, and gardens. It is one of the most versatile toads in the state and the most versatile in Cleveland County.

Most specimens which have been found are typical of the subspecies. However, some have been taken in the Oak—Hickory Association which approach closely the descriptions of *B. w. fowleri* (Hinkley).

4. *Acris crepitans* Baird

This little frog-like hylid is present in all parts of the county but is strictly limited to moist areas. It is common along ditches and creeks and about cattle-tanks and buffalo wallows everywhere. It is very numerous in and about the sloughs on the Canadian flood-plain. It is often active, even in midwinter when the weather is not too cold, and is most commonly found during the spring and early summer.

It breeds in the water which it frequents, everywhere. However, I do not know of its using buffalo-wallows. In hot dry weather, it frequently migrates during the night from drying pools to others containing more water. Such migrations often cover considerable distances. On the whole, its ecological distribution does not follow the plant-complexes in the county but is controlled by the available water-supply.

5. *Pseudacris triseriata clarkii* (Le Conte)

This species must be very shy and secretive, since I have found it only while it was in breeding congresses. After rains in the spring or summer, such breeding-aggregations prove it to be quite abundant in the county. It breeds in ditches, for the most part, and also rarely in buffalo-wallows. The males often call from close under banks and are very difficult to see and to collect.

I have found this species to be like *B. cognatus* in its ecological distribution in the county; i.e., it is abundant on the prairie, sparingly present on prairie islands in the Oak—Hickory, but not present in woodlands nor on the flood-plain of the Canadian River. It should be noted, however, that Smith (1934) had specimens from woodland in Oklahoma although he gives no detailed account as to the type of woods.

6. *Pseudacris occidentalis* (Baird and Girard)

Ortenburger (1926) reported this species from Cleveland County. I have not succeeded in finding it during extensive local collecting and therefore conclude that it must be quite rare here. Since there is still some question as to the validity of this species (Wright and Wright, 1933), it is possible that I have included some specimens of *Ps. t. clarkii* which others might call *Ps. occidentalis*. This does not seem likely, however, inasmuch as nearly all of my specimens have been calling males (and all others females which were taken with them); and the calls of all were similar and distinctive. It is possible that the unknown species of *Pseudacris* mentioned earlier which I have heard calling from buffalo wallows, flooded fields, and the sloughs along the Canadian River (but not anywhere in the Oak—Hickory Association) may be *Ps. occidentalis*.

7. *Pseudacris streckeri* Wright and Wright

This species occurs abundantly in all wooded areas of the country and sparingly in the prairie. Its breeding habits have not been studied carefully in this region. Its distinctive call has been heard from muddy cattle-tanks, flooded fields and ditches and from the sloughs on the Canadian flood plain. It breeds earlier than all other species in the county except *Rana sphenocephala*. The earliest date upon which I have heard calling males of this species is Feb. 26; the latest, May 13. Most breeding occurs in March and April. A female, which laid in the laboratory, produced a clutch of 108 eggs. The breeding of this species is not dependent upon the coming of rain, although a heavy rain greatly stimulates it. It will breed in water as cold as eleven degrees centigrade.

Ps. streckeri is a very shy species and quite difficult to capture. It is also secretive and seldom seen except when its breeding calls announce its presence.

This species was first reported from Cleveland County by Ortenburger (1926) under the name of *Ps. ornata*.

8. *Hyla versicolor versicolor* (Le Conte)

Hylas are very abundant in the Oak—Hickory Association, occurring in about equal numbers in the savannah and bottomlands. I have not found

them elsewhere in the county, even though one would expect that, if merely the presence of trees were the deciding factor in their occurrence, a highway would be provided for their dispersal up the Canadian River from the Oak-Hickory in the southeastern part of the county (see Fig. 1).

They breed in the tanks in the woodland pastures and also in muddy ditches. Males call from the banks of pools or from trees near the water. Mating also occurs out of water and a clasped pair may remain on the bank for some time before entering the water to deposit eggs.

Many individuals have been collected and all are essentially alike in being smooth-skinned. Because of this, these *Hylas* were first thought to be *H. v. chrysoscelis* (Cope). Later, it was concluded that they represent *H. v. versicolor* because of two facts: (1) the call is indistinguishable from that of the

Fig. 1. Generalized vegetation map of Cleveland County, Oklahoma.

latter, and (2) tadpoles reared to an advanced stage from eggs laid by a pair collected while clasped conformed to the description given by Wright (1929) of larvae of *H. v. versicolor*. Whether this means that *H. v. chrysoscelis* does not represent a true subspecies, as some have maintained, or not, was not ascertained.

9. *Microhyla (Gastrophryne) carolinensis* (Holbrook)

A few specimens which have been taken in the Oak—Hickory Association are doubtfully referred to this species primarily because of their call. Only males and emerging young have been found. The call seems lower in pitch than that of *M. olivacea*. It is a deep buzz with no opening note of other type. They breed in muddy cattle-tanks and ditches.

10. *Microhyla (Gastrophryne) olivacea* (Hallowell)

The Texas narrow-mouthed toad is very abundant in all parts of Cleveland County except on the flood-plain of the Canadian River, where it apparently does not occur. They hide beneath stones or other objects during the day and seek food during the night. They breed after rain at any time from early May to late August. May 8 is the earliest, and August 15 the latest dates upon which I have heard calling males in the county, although in other parts of Oklahoma I have found them breeding as late as August 23. Breeding sites include grassy temporary pools, buffalo-wallows, ditches and muddy cattle tanks, but always places of shallow water. Males often start calling at dusk. In a large congress, each male moves about for some time in the early evening, calling once or twice in a place. Later, each finally selects one station which it does not ordinarily leave unless disturbed and continues to call until nearly daylight unless a female is secured. The call is distinctive—a slight and very short "peep" followed immediately by a high-pitched buzz of short duration. The call does not carry far and one needs to be quite near to distinguish the characteristic opening note. Females enter the breeding-pools individually during the night, apparently as a response to the calls of the males. Eggs are usually laid after midnight but apparently always before daylight. Embryonic development is quite rapid in the warm water of the pools, especially in summer—eggs often hatch in less than twelve hours. The metamorphosing young have strong nocturnal instincts, in which they differ from the *Bufos* of the region. Those which emerge during the day immediately hide under appropriate objects and finally disperse from the pool during the second or third night after they leave the water.

11. *Rana catesbeiana* Shaw

Bullfrogs are abundant in artificial lakes, the larger cattle-tanks, and sometimes in deep ditches, especially if near the larger streams. They are especially abundant in Crystal Lake near Norman and along Little River in the Oak—Hickory but they occur in all parts of the county where there is sufficient water. They often migrate at night from pool to pool and are commonly seen on roads far from deep water during these movements. They breed at least in May and probably later.

12. *Rana sphenocephala* Cope

Grass-frogs are common everywhere in the county wherever there is standing water. All adults that I have seen (at least several hundred) have the long snout of *R. sphenocephala;* however, some small specimens could not be distinguished with any degree of certainty from *R. pipiens pipiens* (Schreber). Ortenburger (1926) did not report the latter subspecies from Cleveland County in his summary of the Amphibia of the state although he did report it from several counties to the west and south. I have also seen frogs which I took to be *R. p. pipiens* in other regions of the state, in all directions from Norman and there seems to be no reason why it should not be in Cleveland County, except that it has not been found. On the other hand, if it were at all common I should have found it during my extensive collecting in the area, or at least heard it in the many extensive breeding congresses of grass-frogs which I have studied. It is my conviction at the present time that, if the two frogs in question are really specifically distinct, *R. sphenocephala* is the only one represented in the county, but why this should be so I have no idea.

These frogs breed from late February, at least to mid-August and they are not at all dependent upon rains. The breeding call is something like that of *R. p. pipiens* but appears to me not so loud and raucous. Of the various types of breeding sites listed earlier, only buffalo-wallows are apparently not used at least sometimes by members of this species. Breeding activity is especially notable in cattle-tanks, deep ditches, and the sloughs on the Canadian River during March and April of most years. The tadpoles are agile and hard to catch, especially when full grown. Their habit of frequenting fairly deep water often saves them from death as pools disappear by evaporation, although it does not always do so as is seen from what follows. Metamorphosis of the tadpoles may be hastened by rapid evaporation of a pool (or by some condition associated with this). Below are some observations made on the Canadian River in the spring of 1939 which illustrate this.

On May 4, a deep pool was all that remained of a tract of about two acres, flooded earlier, in which eggs had been found. No tadpoles could be seen in the pool proper, but a shallow arm of it about six feet long was a seething mass of tadpoles. Each larva was struggling toward the edge of the water so that a rim of animals, two or three deep, was present about the edge, and the center of the pool contained only those which could find no room at the rim. At this time, there was a shallow connection to the main pool but no tadpoles crossed this to the deeper water. A few hours later, this arm became cut off from the main pool by evaporation, trapping the tadpoles in no more than one-half inch of water. At this time observation showed that some of the larvae were in metamorphosis, a few with both sets of legs; but the majority showed no evidence of transformation. The most interesting thing was, however, that all of the tadpoles were no more than one-half the size usually attained by tadpoles of this species before metamorphosis. The following morning, practically all the water had disappeared and the former small pool was delineated by masses of dead and dying tadpoles. I found none which had succeeded in transforming in time to escape death. Evidence was abun-

dant that this same phenomenon had occurred elsewhere as the large flooded region had been cut up into small pools with the falling of the water-level. Fifteen former pools, each with a rim of dead tadpoles and a space in the center containing fewer of them were found within an area of about one-half acre of the moist sand.

The adults of *R. sphenocephala* are like the bullfrogs of the region in that they commonly migrate over considerable distances at night. This is only what might be expected, of course, in view of the well-known proclivity of the American grass-frogs in general to range through fields and meadows, even during the day, to feed.

13. *Scaphiopus bombifrons* Cope

S. bombifrons is very numerous in all grassland areas in the county and is present but not abundant in the Oak—Hickory savannah. It has never been seen nor heard on the Canadian flood-plain, nor in the woodland along its border. It is a strictly nocturnal species but is not so difficult to find as is often stated, for I have found it many times on moist roads at all hours from ten P.M. to two A.M. at times when it was not breeding.

It breeds after heavy rains in spring or summer in temporary pools, usually of some extent. It also uses buffalo-wallows and, more rarely, ditches. Flooded fields are a favorite breeding site and very large congresses are often heard in them after spring rains. They also breed in cattle-tanks, although usually not in great numbers. Trowbridge and Trowbridge (1937) presented some evidence that there is a definite breeding season which, however, is modified by the coming of rain. They also reported a single case of a breeding congress in the daytime following a two-inch rain. In view of this, it may be of interest that the only congress among the spadefoots at Norman in the spring of 1939 came in the forenoon of June 28 after a heavy downpour the preceding night. The height of the congress came at about nine A.M., just after rain ceased falling. A few males were still in evidence at eleven, in bright sunshine, but by two P.M. the spadefoots had disappeared entirely. That night, despite the fact that most of the other Anura of the region were breeding in numbers, not a single spadefoot was seen or heard.

All references in my former papers to the spadefoot of this region should be *S. bombifrons* and not to *S. Crammondii* which apparently does not occur here.

14. *Scaphiopus holbrookii* (Harlan)

The eastern spadefoot occurs in the Oak—Hickory Savannah directly east of Norman but I have found it elsewhere in the county. Two small specimens were picked up here from a sandy road on the night of May 10, 1939. These are all that are known from Cleveland County at the present time, but another was found later beside a clear-water pool about three miles east of the western

edge of Pottawatomie County. Nothing is known about the habits of this species in this region. If *S. h. huerteri* (Strecker) be recognized as a valid subspecies, it is probable that my specimens should be referred to it. This is especially true, since Mrs. Helen T. Gaige has written me that the University of Michigan has specimens identified as belonging to this subspecies from southern Cleveland County.

Summary

We may summarize all that is known about the ecological distribution of Anura of Cleveland County, Oklahoma, as follows:

A. Universally distributed in proper microhabitats.

1. *Bufo woodhousii woodhousii* (Girard).
2. *Acris crepitans* Baird
3. *Pseudacris streckeri* Wright & Wright
4. *Rana catesbeiana* Shaw.
5. *Rana sphenocephala* Cope.

B. Limited to the Oak—Hickory Association, eastern Cleveland County.

1. *Bufo americanus americanus* (Holbrook), dwarf form.
2. *Hyla versicolor versicolor* (LeConte).
3. *Microhyla carolinensis* (Holbrook)
4. *Scaphiopus holbrookii* (Harlan).

C. Limited to grassland or to prairie islands in woodland.

1. *Bufo cognatus* Say
2. *Pseudacris triseriata clarkii* (Le Conte)

D. Limited to grassland and Oak—Hickory Savannah.

1. *Microhyla olivacea* (Hallowell)
2. *Scaphiopus bombifrons* Cope

E. Uncertain forms.

1. *Pseudacris occidentalis* (Baird and Girard)
2. *Pseudacris* sp. (in grassland and on the Canadian flood-plain).

TABLE 1.—Live measurement in mm. to the nearest 0.5 of 25 adult male *Bufo americanus americanus* (dwarf form) from eastern Cleveland County, Oklahoma. t.l., total length; h.w., head width; th., length from knee to anus; f.l., foot length; s.l. shank length; interpar. int., interparatoid interval (a, anterior; m, middle; p, posterior level); l.l., length from heel to anus; tym., diameter of tympanum; par.l., length of right paratoid; e.l., diameter of eye; l.so.c., length of superobital crest; p.o.c., length of postobital crest; intn.d., internasal distance.

						interparotoid interval									
t.l.	h.l.	h.wd.	th.	f.l.	s.l.	a.	m.	p.	l.l.	tymp.	par.l.	e.l.	lso. c.	p.o.	intn. d.
61.0	19.0	23.0	22.0	35.0	20.0	10.0	8.0	13.0	77.0	5.0	12.0	8.0	7.0	5.0	....
57.0	18.0	21.0	16.0	31.0	20.0	10.0	8.0	12.0	65.0	4.0	18.0	6.0	8.0	5.0	....
53.0	17.0	18.0	20.0	33.0	18.0	11.0	9.0	12.0	71.0	4.5	11.0	5.0	5.0	4.0	....
56.0	16.0	21.0	19.0	32.0	20.0	11.0	8.0	13.0	71.0	4.5	13.0	6.0	4.5	4.5	....
59.0	17.0	21.0	20.0	33.0	19.0	12.0	5.5	13.0	72.0	5.0	14.0	6.5	8.0	5.0	....
62.0	16.0	23.0	21.0	36.0	22.0	12.0	9.0	12.0	79.0	4.0	14.0	6.0	7.0	5.0	3.0
50.0	13.0	18.0	14.0	30.0	18.0	9.0	8.0	11.0	62.0	4.0	10.0	5.0	6.0	5.0	2.5
56.0	15.0	21.0	21.0	34.0	19.0	11.0	9.0	14.0	74.0	4.5	12.0	6.0	6.5	5.0	3.0
57.0	13.0	22.0	19.0	34.0	21.0	11.0	10.0	17.0	74.0	5.0	12.0	6.0	6.0	5.0	3.0
57.0	14.5	20.0	19.0	31.0	19.0	11.0	8.0	14.0	69.0	5.0	12.0	5.0	8.0	4.0	3.0
57.0	16.0	20.0	22.0	32.0	20.0	10.0	9.0	17.0	74.0	5.0	12.0	6.0	8.0	6.0	3.0
57.0	15.0	21.0	21.0	34.0	23.0	11.0	10.0	14.0	78.0	4.0	12.0	6.0	7.0	7.0	2.5
57.0	16.0	20.0	22.0	34.0	21.0	11.0	9.0	17.0	77.0	5.0	13.0	6.0	8.0	5.5	3.0
57.0	17.0	20.5	22.0	30.0	20.0	11.0	8.0	12.0	72.0	4.0	11.0	6.0	8.0	4.5	3.0
56.0	17.0	21.0	21.0	35.0	20.0	11.0	8.0	13.0	76.0	4.5	12.0	7.0	7.0	5.0	3.0
59.0	17.0	22.0	23.0	35.0	22.0	11.0	7.0	11.0	80.0	5.0	12.0	6.0	6.0	4.0	2.5
59.0	18.0	22.0	22.0	35.0	22.0	11.0	8.0	14.0	79.0	5.0	14.0	5.0	7.0	5.0	3.0
57.0	17.0	22.0	21.0	32.0	21.0	11.0	7.0	12.0	74.0	4.5	12.0	6.0	6.0	5.0	3.0
60.0	17.0	23.0	22.0	32.0	21.0	11.0	8.0	12.0	75.0	4.5	12.0	6.0	8.0	5.0	3.0
52.0	15.0	19.0	16.0	31.0	19.0	11.0	8.0	10.0	66.0	4.0	11.0	5.0	8.0	6.0	3.0
50.0	16.0	20.0	21.0	29.0	20.0	11.0	8.0	10.0	70.0	5.0	11.0	5.0	5.0	4.0	2.5
59.0	16.0	21.0	20.0	33.0	21.0	10.0	8.0	11.0	75.0	5.0	12.0	6.0	8.0	4.0	3.0
60.0	16.0	23.0	23.0	35.0	21.0	11.0	8.0	11.0	79.0	4.5	12.0	6.0	8.0	4.5	3.0
51.0	16.0	19.0	18.0	30.0	19.0	10.0	8.0	10.0	67.4	4.0	10.0	5.0	6.0	5.0	2.5
64.0	20.0	25.0	22.0	35.0	22.0	11.0	7.0	11.0	79.0	6.0	13.0	7.0	9.0	5.0	3.0
56.9	16.3	21.1	20.3	32.8	20.3	10.8	8.1	12.6	73.4	4.5	12.3	5.9	7.0	4.9	2.9

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The Feeding of Ground Beetles

W. Wren Shough

Although the Carabidae or Ground Beetles are largely predaceous in habit, Forbes has shown by studying the contents of the intestine that certain species exhibit different feeding habits.

Several questions may be asked regarding the feeding of ground beetles. What do the beetles eat, how do they attack, and how do the prey defend themselves? Is there a relation between the size of prey and the predator and finally is there any evidence of cannibalism?

Since the observation of feeding in a natural environment is exceedingly difficult, caged specimens were used in my experiments and therefore the conclusions drawn may not be final in all cases.

Methods

The beetles were collected by a painstaking search of all suitable habitats, the best of which was found to be rows of freshly mown clover or alfalfa hay since it still has in it or under it, the various insects that have been feeding on the living plant. In hay that has been allowed to lie longer, these insects die off due to the lack of proper food (some, no doubt, migrate) and thus a food supply for the beetles is lacking.

Another interesting fact worth noting is that in only two cases were beetles *(Pterostichus substriatus)* found living under stones with ants.

The beetles were placed in finger bowls in a thin layer of moist sand, three or four individuals of the same species to a bowl. Later moistened filter paper was substituted for the sand since the filter paper could be easily removed when necessary, improving sanitation. The larger and more active beetles tore the moist paper badly in sucking out the moisture to satisfy thirst, but since the paper was changed after feeding, this tearing presented no great difficulty.

All forms delighted in hiding under the paper, but this was checked by pushing the moistened paper firmly against the bowl, making it more difficult for the bettles to get under.

The beetles were fed on Tuesdays, (occasionally on Wednesdays) and on Fridays of each week at about four P.M. A great variety of foods was obtained by sweeping with an insect net, such as plant-eating insects, spiders, moths, bees and wasps, Lady Bird Beetles, etc. Ants, earthworms, sowbugs, and various ground dwelling forms were also used as food sources. Every effort was made to keep the food forms as lively and as normal as was consistent with collecting and carrying methods. Some preliminary tests in feeding were made with common food substances in order to note the food toleration of the beetles. The results are given in tabular form (Table 2). The number of the beetles collected, number dying, and some general observations as to their behavior in captivity are given in Table 1.

TABLE 1.—Observational Data

Name of Beetle	Length mm.	Length inches	No. Coll.	No. Died	Behavior in Captivity	Cannibalistic tendencies
Amara impuncticollis	7–9	5/16-6/16	16	10	quiet but alert	none
Calosoma calidium	21–23	14/16-15/16	11	4	nervous, excitable	fought at times
C. scrutator	28–30	1 1/8-1 1/4	1	0	quiet	?
Evarthrus sodalis	15–17	5/8-6/8	31	18	active but easily frightened	very high
Harpalus caliginosus	21–25	7/8-1	58	10	quiet unless disturbed	occasional
H. pennsylvanicus	13–15.5	1/2-5/8	11	3	quiet	none
Pterostichus convexicollis	10–14	7/16-9/16	6	3	active, alert	slight
P. lucublandus	10–14	7/16-9/16	10	6	active, alert	a little
P. substriatus	12–14	1/2-9/16	23	19	active	high
Pasimachus elongatus	23–26	15/16-1	15	1	quiet except at feeding and in evening	fought occasionally

TABLE 2.—Food Preferences

Beetle	Cheese	Boiled White of Egg	Boiled Yolk of Egg	Lean Meat	Fat Meat	Banana	Boiled Wheat	Dry Wheat	Peach
Amara impuncticollis	*	0		0	0	*	*	0	*
Calosoma calidum	*	0	**	*	0	**	0	0	
C. scrutator		0	0				0	0	
Evarthrus sodalis	*								
Harpalus caliginosus	*	0	*	0	*	*	***	0	***
H. pennsylvanicus	*	*	*	**		**	*	0	0
Pterostichus convexicollis							*	0	
P. lucublandus				***			**	0	
P. substriatus			*				*	0	
Pasimachus elongatus	**	0	*	*	0 ?	0	0	0	*

* Eaten, degree by number of *'s. Blank spaces are left where the test was too short to be conclusive.
0 Refused
? Doubtful

Observations

Calosoma calidum Fab.—This form is nervous in captivity, feeding fitfully when non-living food is given. It fights and tears at edge of paper, until the paper is in shreds.

On the other hand, with living food *C. calidum* showed more speed and accuracy of attack than did any of the other beetles in the collection. Katy-did nymphs were seized instantly on their arrival in the cage. The beetle showed complete mastery and acted greatly excited at the prospect of food. Its first grip was made at the middle of the Katy-did's abdomen, but when the Katy-did made no struggle and showed no defensive action, the grip was shifted to the thorax just back of the head. The beetle immediately started feeding and buried its head to the eyes in the thorax of the feebly kicking Katy-did. (The mandibles knead the food and the maxillae carry it to the mouth.)

Stone crickets were left in the cage with *C. calidum* for a week and, with one exception, were not killed. The long antennae of the stone cricket made a very efficient warning device, enabling it to keep at a distance from the beetle, and its long, spined, hind tibia served to protect its abdomen from the charges made by the beetle. The antennae of one cricket were removed, thus permitting the beetle to get closer, but the legs were still a defense, sudden jumps of the cricket confusing the beetle to a considerable extent. However, the following morning, the scattered skeleton of the cricket was found.

Stink bugs were taken by *C. calidum* without a change of attitude although the odor was extremely nauseating. They were attacked at the corner of the thorax, the grip being shifted later to the dorsal side of the abdomen. Scattered skeletal parts, wings, legs, tergites, were all that were left uneaten.

A cicada nymph was eaten during one night. The attack was again at the dorsal side of the abdomen. Excepting the entry opening made by the jaws of the beetle, the skeleton remained intact.

A large black ant was thrown into the cage with *C. calidum* and taken instantly. This ant had been with *Harpalus pennsylvanicus* for two or more hours without even being investigated by those beetles.

When extremely hungry, *C. calidum* would take sowbugs, but never if anything else was offered at the same time.

Jumping spiders were freely eaten by *C. calidum,* the spider making no defense of any value. It was possible for *C. calidum* to reach the top of the cage, by rising on the hind legs, thus an advantage was given in an attack on climbing food forms. Such an advantage would, of course, not be given in a normal environment.

The quietness of a small butterfly chrysalis protected it from the notice of the beetle for a period of fifteen minutes. Eventually the beetle happened (?) on to the chrysalis, immediately punctured it and "sucked out" the contents.

C. calidum showed a marked preference for all sorts of larval forms.

While, unfortunately, it was impossible to obtain the larger moth and butterfly larvae, "measuring worms" were plentiful enough to use as a source of food. The method of defense of these larvae, consisting of a series of "back-flips" caused by a sudden flexion and extension of the body, was never successful in overcoming or rather evading the sudden and vicious attack of *C. calidum*. The "worms" were grasped in the mandibles at a mid-dorsal point, lifted clear of the cage floor and consumed entirely.

Evarthrus sodalis Lec.—Forbes found, through dissection, that the food of this beetle consists of canker worms and caterpillars to the extent of 93% of all the food taken.

Living food thrown into the cage was the signal for intense excitement on the part of the beetles. They fought viciously with each other over bits of food. These fights frequently became so furious and personal that the combatants forgot the food altogether. In such cases, the food was immediately appropriated by a third beetle.

Small grasshopper nymphs were unable to cope with the attack of the beetle in any fashion, but larger nymphs defended themselves with vigorous kicks and by jumping.

Leaf hoppers were difficult prey for *E. sodalis* because of their skeleton and the shield made for the abdomen by the wings. After investigating the hoppers *E. sodalis* commonly attacked the legs or the corners of the thorax where a good grip was possible. The strong jumping abilities of the leaf hoppers defended them against attack again and again. The complete bewilderment of the beetle was amusing to watch, since the hopper was there before it and then suddenly and mysteriously gone. If the hopper were slow in recovery at the finish of a jump another beetle was upon him at once.

"Stink bugs" were taken by *E. sodalis*, the beetle showing no discomfort at the odor. The bugs were grasped at the corner of the pronotum and, with the exception of the wing covers and wings, legs and harder skeletal parts, completely consumed.

E. sodalis was very active in captivity and showed but little fear or nervousness. They were intensely cannibalistic, over half of the collection being eaten by their fellows.

Harpalus caliginosus Fab.—According to Forbe's dissections and other observations (Webster) this form is, at times, a plant (seed) eater of possibly economic importance. It has been seen to eat Gypsy moth larvae (Burgess). The beetles are quiet in captivity, resting, calmly in the cages, tending to pile up on the side away from the light.

From a variety of food insects placed in the cages *H. caliginosus* selected the "inch worms." Due to the handicap of size the inch worm had no defense, excepting the "back-flip."

A tree cricket *(Oecanthus)* was grasped by the abdomen, and a tug-of-war ensued, ending when the abdomen was torn from the cricket.

The short and thickened mandibles of *H. caliginosus* slid off leaf hoppers without penetration. The jumping of the leaf hoppers was highly disconcerting to the slow deliberate beetle.

Inch worms were enabled to save themselves for a considerable period of time by their use of the "back-flip," but their loss of control upon landing left them open to attack when confined with several beetles.

When ant pupae were placed in the cage, *H. caliginosus* sorted them over methodically, taking some and rejecting others without any apparent reason. At the end of a 22 hour period, the five beetles in one cage had eaten between 500 and 600 pupae, although other food, (active living forms) was present. The beetle lifted the entire pupa in its mandibles, kneading it slowly and wholly consuming it.

"Stink bugs" were investigated over and over but none were taken as far as could be determined, although they were left in the cage long periods of time, over-night in most cases.

An angle worm was partially eaten after it had quieted and released less slime. It appeared to be distasteful.

From the behavior of this beetle, it may be concluded that they prefer plant food and take only the quieter forms of animal life.

Harpalus pennsylvanicus Dej.—So far as feeding habits are concerned this beetle may be called a smaller edition of *H. caliginosus*. A large butterfly larvae taken from sweet clover was in the cage with eight *H. pennsylvanicus* beetles for two hours and was not molested or even investigated in that period. It was removed and some small inch worms thrown in. The inch worms were immediately taken. It is possible that size correlation was responsible for this action. Most beetles hesitate before attacking food animals that greatly surpass them in size.

Pterostichus convexicollis, P. lucublandus Say.—Their alertness and activity makes collection of these forms difficult, for it is hard to pick them up without injuring them. Many of those collected were found dead when collecting jars were opened in the laboratory. Those still living, continued to live contentedly in the cases provided, as was the case with all the smaller species collected. There was, however, a considerable degree of cannibalism.

P. convexicollis and *lucublandus*, as has been said, had an agility and alertness which placed them second only to *Calosoma calidum* in speed and accuracy of attack. Like *C. calidum*, they showed a marked preference for larval forms as food.

"Inch worms" or "measuring worms" were taken by these beetles, sometimes so suddenly that the "worm" had no time to defend itself by the "back-flip." At other times the beetle followed the worm closely, capturing it when it lost control in landing at the end of a flip.

P. lucublandus unhesitatingly attacked moth or butterfly larvae three times its size. These larvae fought back with a characteristic whipping motion of the anterior of the body. The beetle's attack was made on the posterior part of

the larvae, the beetle running back with agile movements when menaced by the head of the larvae. The attacks continued in a series of dashes, the beetle tearing an opening in the skin of the larva almost every time he came in. The larva grew successively weaker so that the beetle became emboldened and stayed in. As the greatly weakened larva gave up the "whipping" and attempted only to crawl away, the beetle, joined by others in the group, began feeding on the body liquids oozing from the wounds. Only the integument was left when the feeding finished. These beetles may be possibly be classed among the more beneficial of the family, although the eagerness with which they fed on boiled wheat in the preliminary feeding appears somewhat suspicious.

Pterostichus substriatus Lec.—The habits of this beetle in feeding and its choice of food show little divergence from those of the typically predacious members of the family, the eating of boiled wheat being the exception. They preferred larval forms as their living food supply.

A detailed description of the attack of *P. substriatus* on strong grasshopper nymphs can be taken as general for the attack of all ground beetles upon strong and active prey. Fresh, uninjured nymphs in the next to last instars were dropped into the cage and were immediately attacked by the beetles. The nymphs jumped and kicked vigorously. When a jumping leg was torn from the nymph one beetle began to feed upon it, while another continued the attack on the grasshopper, finally getting a grip with the mandibles just back of the head. The beetle clung tightly with mandibles and legs, riding the grasshopper, which soon quieted. Feeding was begun on the abdomen and only scattered skeletal remains were left.

Pasimachus elongatus Lec.—*Pasimachus elongatus* lived quietly in captivity, even under crowded conditions. As is shown in Table 1, only one died out of fifteen collected. Whether this was due to cannibalism, I was unable to determine.

The extremely sharp, elongated mandibles make this beetle a chief predator equal to *Calosoma calidum*. In preliminary feeding, it showed a marked appetite for animal food as is shown in Table 2 below. On living food forms no selection was evident, every item offered was taken. The mandibles were long and sharp enough to penetrate the exoskeleton of every insect placed in the cage.

The most interesting act observed in the case of *P. elongatus* was the intense excitement displayed upon the arrival of food. Although the beetles were extremely calm, even "sleepy" at other times (during the day), when food was placed in the cage, they quivered with excitement. The attack was a vicious onslaught, the mandibles being driven home into the softer part of the prey, and inflicting enormous wounds. In case the prey escaped and limped away, the beetle seemingly became maddened and blinded, dashing about the cage, biting the other beetles, tearing up the paper floor covering in a ferocious manner. In such cases, the beetle would frequently stop and throw its head up and back with the mandibles wide spread, giving a ludicrous similarity to an African Cape Buffalo in a rage. Quiet was restored only when the beetle

again located his prey. The food animals were torn to fragments, the softer parts eaten, only the hardened or juiceless fragments being left, as the exoskeleton, wings and elytra of beetles.

Amara impuncticollis Say—The size of these beetles makes them difficult to observe so far as feeding is concerned but one habit is worthy of note. They will attack larval forms of Lepidoptera five or six times their own size. The attack is made on the dorsal side of the larvae, the beetle holding on with both mandibles and legs. No matter how the "worm" twists and turns the beetle clings. If the beetle is unable to penetrate the body wall of the larvae, he loses interest for a time but may return again and again to try his luck. Sooner or later the beetle breaks through, other beetles join in the feast and the event is finished.

Discussion

The observations show that among the types of living animal food offered, the carabid beetles have little or no food selectivity, any form that can be penetrated is eaten, although larval forms are given a wide preference, due, I believe, to ease of capture and softness of body. Certain of the beetles, notably *Calosoma* sp. and *Pasimachus* sp. are definitely carnivorous, others, as *Harpalus* sp., *Evarthrus sodalis*, and *Nothopus grossus* feed to a varying extent on plant food, though none seek plant food exclusively. Insects are usually taken at the abdomen; large insects, etc., are gripped first at the back of the head, later the grip is shifted to the abdomen. The point of attack seems to depend largely upon the difficulty with which the prey is subdued. With no battle in prospect, the beetle attacks the abdomen, as the softest and easiest place to make a quick entrance to the food.

The fact that bugs are, almost without exception, attacked at the corner of the thorax is explained by the obvious fact that this is one of the few places where a beetle can get a desirable grip on the bug. In general, I cannot believe that the odor of the bug is repellent to the beetle.

Defense against the attack of the beetles was inadequate in almost every case. Active insects are able to evade the attacks of the slower beetles and this would be of great importance in a natural environment. Since the beetles are attracted by motion, "freezing" and protective coloration no doubt protect many insects in a natural setting. This effect, of course, cannot be observed in captivity where conditions are changed so greatly from the original environment.

Many of the carabidae are rather poor climbers confining their depredation to ground forms. However, some of the beetles are fair climbers where the substrate is sufficiently rough to provide an adequate foothold. Adult climbing insects, with greater climbing ability, would be enabled to escape the earth beetles, but the slower larval forms would fall victims surely. Unfortunately, the most efficient climbers, *Harpalus caliginosus* and allied forms, are essentially plant feeders, although even these would probably prefer larvae of destructive Lepidoptera when extremely plentiful, such as canker worms.

The slime of slugs and earthworms is distinctly unpleasant to the earth

beetles but does not prevent a hungry beetle from making a meal. The beetle retires, removes the slime from the mandibles and returns again to the food animal. This may be repeated many times. However, the beetle must be hungry to attempt such a meal.

The size and activity of the prey determines to a greater extent whether or not the beetle will attack. Slow, inactive animals are attacked even when the size is 3 or 4 times that of the beetle. The beetles were never seen to attack an active form much larger than themselves, excepting in the case of crippled grasshopper nymphs and even in this case the nymphs were exhausted from jumping in the close confines of the cage.

Cannibalism in captivity is correlated with crowding and activity. Quiet beetles can be safely crowded, but active forms are more likely to survive when only two or not more than three are in the same cage.

Summary

1. Beetles studied in captivity are shown to be non-specific in selection of food.

2. The attack of the beetles varies in form; a relation in relative sizes of the predator and the food form was found.

3. Locomotion, i.e., climbing, jumps and kicks were found to be the most effective forms of protection against carabids in captivity.

4. Larger beetles will eat small food forms, but small beetles attack only the larval forms of insects bigger than themselves.

5. Cannibalism was correlated with crowding and activity.

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Did the Peckhams Witness the Invention of a Tool by Ammophila urnaria?

John A. Frisch, S. J.

In the year 1898 the Peckhams reported that they had observed a wasp, of the species *Ammophila urnaria* (now named *Sphex urnarius*), repeatedly employ a pebble to pound down the soil used in closing the tunnel of her nest; they concluded that they had witnessed a unique event, the improvising and the intelligent use of a tool by an insect. A drawing of this *Ammophila*, in the act of using the pebble as a tool, accompanied their report. This drawing has since been copied in many textbooks of biology and psychology, and it is usually supplemented by the statement that this *Ammophila* was the first insect to improvise a tool. As no mention is made of any wasp using a tool since then, the inference is that this individual Ammophila of the Peckhams was unique indeed, and had neither predecessors nor successors in the use of a tool. Among the more recent authors, who have either reproduced the drawing, or who refer to the observations of the Peckhams are, Wheeler (1923, 1928), Thouless (1927), Wyatt (1930), Shumway (1931), Metcalf and Flint (1932), Folsom and Wardle (1934), Cockerell (1935), Williams (1937), Aaron (1938).

The reception given this discovery by the naturalists is exemplified by Hingston (1929): "To my mind it forms the best instance of intelligence recorded in any insect." The psychologists were even more sanguine. McDougall (1923) says: "Oh wonderful Ammophila! What shall Fabre or Bergson or the mechanists say to this most irregular behavior, so upsetting to every theory except the common sense theory that instinct and intelligence cooperate most intimately and that, while the wasp has much instinct, she also has some intelligence. Here is *Ammophila* using a tool! A mode of behavior commonly regarded as the exclusive prerogative of man, sometimes proposed as defining the mark of his species."

The sole question I wish to investigate here is, "Did the Peckhams witness the actual invention of a tool?" For the Peckhams to have witnessed the improvising of a tool, the two following conditions would have had to be present: a) that no wasp, or at least no wasp of the species *urnaria* had ever before used a pebble or other solid object as a tool to pound the soil, and b) that this particular wasp of the Peckhams regularly employed this method, so as to make certain that her behavior was not an accident, but a designed and intelligent procedure.

The second condition was not fulfilled. The Peckhams did not observe their wasp further, perhaps because they erroneously thought that she builds only one cell to her nest. I have found two cells to the nest and have known the wasp to work at her nest for five days. If the Peckhams had known more

about the habits of *urnaria* they could have observed the wasp further to see whether she repeated her supposedly unique behavior.

Nor was the first condition fulfilled, namely that no wasp, at least of the species *urnaria* had ever before used a pebble or other solid object for pounding. Sometime after their observation of their supposedly unique *urnaria,* the Peckhams saw a note of a similar but much earlier observation by Williston (1892) on *Ammophila yarrowi* Cres. But they mistakenly interpreted Williston's account as referring to a single individual. Williston says that the wasps "were so numerous that one was distracted by their multiplicity, but by singling out different individuals we were able to verify each detail of their operations." He then pieces together the isolated observations made on different individuals into a composite whole—the wasp after digging the nest, selects a door stone, places it in the tunnel and then heaps dirt on it. Still speaking in general terms, and not of a particular wasp, he continues, "When she had heaped up the dirt to her satisfaction, she again flew away and immediately returned with a smaller pebble, perhaps an eighth of an inch in diameter, and then, standing more nearly erect, with the front feet folded beneath her, she pressed down the dust all over and about the opening, smoothing off the surface, and accompanying the action with a peculiar rasping sound. After all this was done, and she spent several minutes each time in thus stamping the earth so that only a keen eye could detect any abrasion on the surface, she laid aside the pebble and flew away to be gone for some minutes." Every time the wasp returned with a paralyzed larva she opened the nest, took the larva down and then closed "up the entrance precisely as before," Williston's concluding remarks leave no doubt that all the wasps were using a pounding pebble: "The thing that struck us as most remarkable was the judgement in the selection of a pebble, precisely the right size to fit the entrance, and the use of the small pebble in smoothing down and packing the soil over the opening, together with the instinct that taught *them* to remove every evidence that the earth had been disturbed." It is evident that in *Ammophila yarrowi* the use of a pounding pebble is a fixed habit or instinct, common to all members of the species.

Also previous to the observations of the Peckhams, another investigator, Pergande, (1892) described some observations he made on *Ammophila gryphus* Sm. He says that the wasp "ran a short distance and picked up with its mandibles a small pebble, carried it to the mysterious spot" (the closed entrance tunnel), "and deposited it on top of it, pressing it at the same time down as much as possible to insure its remaining in position. Running then again a short distance it picked up another pebble and placed it close to the first one; after a while a third was added." Unable to find more pebbles, the wasp "returned to its little mound of pebbles, commenced to rearrange them and to press them again down as much as possible." To the student of the habits of wasps, the term "pressing" is synonymous with the term "pounding!" This wasp, therefore, used several pounding pebbles and left them on the surface of the nest.

Since the time of the observations of the Peckhams, another investigator,

Hartman, (1905) has observed *Ammophila procera.* He says that the wasp uses chips of wood, dry leaves and twigs, besides sand, in closing her nest. "When the nest is full enough for the wasp to reach down comfortably, she presses the separate pieces firmly down before she lets go and accompanies the strenuous occupation with a cheerful buzz. Now it sometimes happens, especially towards the end of the operation, that a piece of wood is pressed down tightly, then pulled out and pressed down again and this repeated several times, so that one might suspect that the wasp were here improvising a tool with which to tamp down the sand."

Hungerford and Williams (1912) report a small species of *Ammophila* using a small stick to pack down the earth and a larger species using "as a tool the tibia and tarsus of a small Acridiid."

The Raus (1918) report that *Ammophila pictipennis* uses clods of soil to fill her tunnel, which she grinds by a rotary or side motion until worn to dust. When she has thus filled the top of the tunnel level with the ground, she selects " a pebble usually a little larger than her head, but sometimes an unusually hard clod or bit of wood," and this she "brings in her mandibles and grasping it firmly, she rubs, pounds and hammers down the dirt on top of the hole until all traces of the fill are obliterated."

Rayment (1935) says: "I venture to assert that the wasp *Ammophila* already has the ability to use a tool, for I have observed her here in Australia to select a suitable stone and then proceed to ram down loose soil just as a human being would do."

It will be observed that none of the above observations refer to *Ammophila urnaria.* Possibly the *urnaria* of the Peckhams was the first of her species to use a tool. My own observations show that *urnaria* uses, besides the finely divided excavated soil, larger lumps of soil, small pebbles and other bulky material in closing the tunnel of her nest. I have repeatedly seen her use bits of wood, twigs and even male pine cones. Thus one *urnaria,* whose nest was under a pine tree, where the ground was littered with broken pine needles and very small male pine cones, examined in turn several pine cones and finally picked one up and rammed it into the tunnel; but she immediately pulled it out again and dropped it aside. Then she selected another cone, rammed it in and left it there. Next she scraped some soil into the tunnel and rammed it down with her head. Then she alternately rammed pine cones and soil into the tunnel. Next she picked up a pebble, rammed it in, but pulled it out and dropped it aside, as though she had used the pebble to pound in the fine soil. She completed her work by alternately scraping soil into the tunnel and ramming in bits of pine needles, which latter she would occasionally pull out again and lay saide. An enthusiastic observer would be justified in maintaining that this wasp had used male pine cones, pine needles, bits of wood, and a pebble to pound in the finely divided soil; in other words had employed them as tools, but that she did not use the same tool twice.

The above observations force the conclusion that all *Ammophilas* thus far observed, including *urnaria,* use solid objects as a pounding tool. At best the

urnaria of the Peckhams could be credited with a more spectacular use of a pebble, namely the repeated use of the same pebble. Must such a more spectacular use be considered the invention of a tool? Hardly. For it is quite possible under the laws of chance that the wasp could use the same pebble several times in succession, by accident and quite unintentionally. Such a chance happening would be particularly likely to occur if bulky material were rare in the vicinity of the nest. The Peckhams' description of the closing of the nest of their *urnaria* creates a strong impression that there actually was little or no bulky material at hand to help in the filling of the tunnel. "In filling her nest she put her head down into it and bit away at the loose earth from all sides, letting it fall to the bottom of the burrow and then, after a quantity had accumulated, jammed it down with her head. Earth was then brought from the outside and pressed in and then more was bitten from the sides. When at last the filling was level with the ground, she brought a small quantity of fine grains of dirt to the spot. . . ." The only two instances, in which I have observed a wasp fill her tunnel by biting away the walls of the tunnel, occurred where there was a definite shortage of excavated soil or bulky material.

Since the use of solid material for pounding is a part of the hereditary equipment of all *urnaria*, the repeated and successive use of the same pebble is quite within the hereditary capacity of the wasp. Even the exclusive use by an individual *urnaria* of a pebble for pounding the soil would not argue the invention of a tool. The habitual use of solid materials, including pebbles, for pounding, could easily result in the exclusive use of a pebble. The memory of neater and quicker work, associated with the occasional use of a pebble, could establish a constantly increasing valence for pebbles, to the gradual exclusion of other material; and if pebbles were rare in the vicinity of the nest, could result in the repeated use of the same pebble, without any direct perception on the part of the wasp of the relation of the means employed to the end to be attained. The invention of a tool postulates just such perception of the relation of the means to the end.

As stated earlier in this discussion, the Peckhams considered their observation the first recorded instance of the use of a tool by a wasp; it was only some time later that they saw Williston's (1892) earlier report of a similar observation. By some queer mental gymnastics, the discovery that the *Ammophila* of the Peckhams was not the first, nor the only wasp to use a pebble as a tool, was hailed by the proponents of the intelligence of this act as a further proof of its intelligence. The Peckhams state, "We are claiming a great deal for *Ammophila* when we say that she improvised a tool and made intelligent use of it, for such actions are rare even among higher animals, but fortunately our observation does not stand alone, although we supposed this to be the case at the time it was made." They then refer to Williston's observation. As we have seen, Williston's observation does not indicate the improvisation of a tool by a single individual, but clearly shows that the use of a tool is a fixed habit of all the individuals of the species *yarrowi*. Bouvier (1922) is also mistaken when he states expressly that Williston's observation concerned only a single individual. McDougall is doubly wrong when he says: "If the Peckhams'

instance stood alone, perhaps it would be wise to dismiss it as a joke, a hoax, or an error of observation or of memory. But unfortunately for the theological, the philosophical, and the mechanical theorists, it does not stand alone. Closely similar behavior, on the part of another member of the same species, has been minutely observed by an independent observer in a distant part of America. Are we then to regard each of these two wasps as a lively "bahnbrechende" genius, leading their species onward to the use of tools; individual sports, comparable to the man or ape, who first took a stone in his hand to crack a nut and so foreshadowed the genius of Nasmyth? I see no other plausible interpretation of the facts." Unfortunately for McDougall, his facts are wrong; Williston's report does not deal with a single wasp, and the wasps belong to a different species.

Finally, there is a lingering doubt in my mind as to whether the *Ammophila* of the Peckhams owes her prowess to her spectacular behavior, or rather to a more spectacular description of her behavior. The Peckhams are proclaimed as peerless observers, seeking only the truth and fully aware of the pitfalls of anthropomorphism. Nevertheless, in all their observations they were intent on proving that the wasps performed intelligent acts, and they consider *Ammophila's* behavior the crowning glory of their proof. Their sentimentality and their humanizing tendencies are evident in all their studies; they interpret every action of the wasps in terms of our own conduct, and motivate their actions in terms of our own motives. Thus, when their "fastidious little creature" had closed her nest, "she stood back and surveyed the hole, and it seemed to us that we could read pride and satisfaction in her mien." Again, "We remember her as the most fastidious and perfect little worker of the whole season, so nice was she in her adaptation of means to an end, so busy and contented in her labor of love. And so pretty in her pride over her completed work." After using the pebble, "the little creature, all unconscious of the commotion she had aroused in our minds, unconscious indeed of our very existence and intent only on doing her work and doing it well, gave one final, comprehensive glance and flew away."

Many of the observations made by the Peckhams were very superficial and led them into wrong conclusions. On the basis of an observation made on a single individual of the wasp *Ammobia ichneumonea* they state that this species builds only one cell to its nest and stores only one grasshopper as food for her offspring. I have shown (Frisch, 1937) that *ichneumonea* builds as many as seven cells to her nest and stores up to five grasshoppers in each cell. The Peckhams came upon their *ichneumonea* on the first day of nest building, after she had constructed the first cell and was storing the first grasshopper. Instead of continuing their observations, they dug up the nest and drew their erroneous conclusions and never checked them. If they had patiently observed the wasp for several days, they would have learned that she closes the nest each evening, but opens it the next morning, and may continue building more cells and storing them for as long as two weeks. This habit of digging up nests without sufficient observation led them into wrong conclusions in other instances.

However, even granting that the Peckhams' description of the behavior of their *Ammophila* is not a glorified version of their observations, but is accurate in every detail, they have made of her a rank impostor. If the adoption of solid objects for pounding is the invention of a tool, the credit for the invention must be given to the first wasp to use this method, somewhere in the dim past of geological history; for the method is now an automatic habit, common to all *Ammophilas* in varying degrees of perfection. Who was this bahnbrechende" genius? Nobody knows; it certainly was not the *Ammophila* of the Peckhams.

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Studies of North American Solpugida, I. The True Identity of Eremobates pallipes (Say)

Edson Fichter

Over a period of 8 years (1932 to 1939, inclusive) the Department of Entomology of the University of Nebraska has acquired 48 specimens (40 female, 8 male) of a single species of Solpugida (Solifugae), *Eremobates pallipes* (Say), from within the state of Nebraska. The majority of these specimens have been received from correspondents in various parts of the state; a few have been collected by the writer. An attempt to determine the specific identity of this arachnid early revealed an inadequate original description and apparent confusion and discrepancies concerning its specific status in the subsequent literature.

An effort is herewith made to render a modern and adequate diagnosis and to establish the true identity of *E. pallipes* (Say). This paper also presents notes concerning the distribution of the species in Nebraska, together with a few observations upon its biology.

It appears reasonably certain that the 48 specimens in this series of Nebraska Solpugida are referable to a single species. It is notable, however, that of the only other species known to occur in Nebraska, only 2 specimens, both males, have been taken. Since the size range of all the females in the collection encompasses the size ranges of the males of both species (body length of 15-21 mm. and 25 mm., respectively), it seemed advisable to scrutinize the series of females in an attempt to determine whether or not it might comprise specimens of the two species. Accordingly, the series of females was divided into two body length size ranges, 14-21 mm. and 22-30 mm. No consistent character was discernible which would point to the presence of two species in this series. Also, while camped in a wide and shallow canyon in the range country of Box Butte County, Nebraska, in the summer of 1939, a member of the writer's collecting party found two Solpugida under dried cow chips. These, the only specimens of Solpugida found in that area at that time, were but a few yards apart on the dry floor of the canyon. One was a male, the other a female. They are now a part of the series herein reported upon. In light of this evidence, it seems reasonable to consider the males and females of this series of Nebraska Solpugida as comprising a single species.

Certain variations do appear in the series, however, which warrant attention. The most markedly variable character is the scopula of papillae on the metatarsus of the pedipalp of the female. It is present in 9 of the 40 females, absent in the remaining 31. Of 35 measurable (not mutilated) females, 19 fall in the 14-21 mm. size range class. Five of these possess a scopula. Sixteen fall in the 22-30 mm. class, 3 of which show a scopula. Every one of the 8 male specimens show a scopula, the number of papillae varying from 45 to

75. This range in number of papillae, and indeed the very presence or absence of them, may be due to loss through mechanical means, though no definite evidence is at hand either in support or denial of this suggestion. The presence or absence of the scopula appears, therefore, to be an unreliable character in differentiating the species of Eremobatidae. The size (body length) variations noted are probably to be accounted for by age.

In one female of the series supernumerary teeth appear on the chelicerae (Fig. 1, G, H). These are readily adjudged as the products of an abnormality, and of no specific significance. Some individuals have excessively worn teeth (Fig. 1, E, F). This may also be the result of age.

Roewer (1934) has split the genus *Eremobates* Banks, 1900, with its 41 species, into 11 genera, chiefly on the basis of the ventral spining of the 2nd and 4th tarsi. Examination of the series of 40 females disclosed an apparent

Fig. 1. *Eremobates pallipes* (Say). Side view of chelicerae showing pattern of dentition.

A. Male upper.
B. Male lower.
C. Female upper normal.
D. Female lower normal.
E. Female upper worn.
F. Female lower worn.
G. Female upper supernumerary.
H. Female lower supernumerary.

variability in the number of what may be recognized as true spines. There is evident a certain degree of general conformity to a species pattern of tarsal spining, but this seems to rely to a considerable extent upon the age of the specimen, i. e., what will have the appearance of a robust, true spine in a large and apparently old individual may be weak and hair-like in a small and presumably young specimen. Furthermore, differences are to be found in the spination of opposite tarsi of the same individual. These seeming variations in the spine patterns of the 2nd and 4th tarsi would tend to invalidate spine patterns even as workable specific characters. Although differences in spine patterns due to age may be more apparent than real, it is needless to say that their use in the separation of genera is questionable, particularly where there appears to exist no supporting generic differences, nor even the need for more genera as an expedient in classification.

On July 6, 1820, Thomas Say, who was a member of Major Long's Expedition from Pittsburgh to the Rocky Mountains, collected specimens of a single species of Solpugida near the mouth of Platte Canyon at the edge of the Rocky Mountains in Douglas County, Colorado, a point some 20 miles south of the present city of Denver. In his diagnoses (James, 1823) he described the female first, naming it *Galeodes pallipes*. Failing to recognize the specific unity of his specimens, he described the male as another species, *G. subulata*. Thus did *Galeodes pallipes* Say become the first named American member of the Solpugida.

Simon (1879) recognized that "the two species of Say, found at the same time, differ absolutely only in sexual characters," and stated that "there is no doubt the second (supposed species of Say's original descriptions) is the male of the first." He therewith redefined the *subulata* male of Say as *pallipes* male, giving both the male and female new and rather detailed descriptions, and relegated the species to the genus *Datames*. Simon also remarked that *pallipes* "has been found in numbers in the vicinity of Denver, Colorado," from which locality he reported having received two specimens.

Kraepelin (1901) wrote: "The description of the female by Say is insufficient; the female described by Simon is that of *Eremobates cinerascens* Koch." It is interesting to note here that the original diagnosis of *cinerascens*, presented by Koch (1842) as *Gluvia cinerascens*, was based upon the male only, from Mexico. With the statement, "only the male known completely," Kraepelin removed *pallipes* to the genus *Eremobates*, and presented a description of what he considered to be the male of this species. Although Kraepelin accepted as valid the male of Simon's *pallipes*, his own description of *pallipes* male does not conform with that of Simon.

Roewer (1934) corroborated Kraepelin's work, considering "the female described by Simon . . . as belonging to *E. cinerascens*." Roewer, too, describes only the male of *pallipes*.

The Nebraska series of Solpugida here considered fits into the above picture in the following manner. The females conform to Simon's description of the

female of *pallipes*. This is especially striking as regards the dental pattern of the chelicerae (Fig. 1, C, D). Indeed, the writer has largely fashioned his description of the female dental pattern after that of Simon. On the other hand, the males of this Nebraska series fail to conform to the description of the male of *pallipes* given by Simon. He described the movable finger of the chelicerae as "armed with a strong compressed tooth . . . preceded by 2 small sharp teeth." In the males of the Nebraska series the movable finger of the chelicera is armed as in the female, with two large (1 front and 1 main) teeth between which are two small (intermediate) teeth (Fig. 1, A, B).

Kraepelin's description of the male of *pallipes* does not conform to that of the males of the Nebraska series. He described a "ventral mandible finger with one proximal main tooth, on which there is sometimes also a tiny front tooth about one-half as high."

Although Say's diagnosis is admittedly inadequate, it seems pertinent to note that he described the movable ventral finger of the chelicera of the female as armed "with about two robust teeth." This suggests the pattern found in the Nebraska series, in both the males and the females.

It is of particular interest to note that Simon indicated the species *pallipes* as having been reported from Colorado, Utah, Nevada, and Kansas, and that two specimens collected in the vicinity of Denver, Colorado (the type locality of *pallipes*) had been sent to him. *E. cinerascens* which Kraepelin stated was described by Simon as *pallipes*, Kraepelin reported as being found in Mexico. Kraepelin then reported his *pallipes* from Mexico, Colorado, Utah, Nevada, and Kansas.

If the records of known localities of 38 of the 41 North American species of *Eremobates* as given by Roewer (1934) are indicated upon a map, it is at once evident that the center of distribution is Mexico (20 species), with somewhat fewer species having been taken in California (12 species). Two species have been reported from Arizona, 1 from New Mexico, 2 from Nevada, 3 from Utah, 3 from Colorado, and 2 from Kansas, both *cinerascens* and *pallipes* having been reported from each of the last four states named. Thereby *cinerascens* would show a remarkable case of discontinuous distribution! Such an apparent condition could arise from the lack of collection records from the intervening areas, where it might in reality occur. If so, *cinerascens* would be the only species in the genus to show such wide distribution in North America.

From the foregoing it is evident that *Eremobates cinerascens* (Koch) is a valid Mexican species. The *cinerascens* of Kraepelin (1901) and of Roewer (1934), from Colorado, Utah, Nevada, and Kansas, is, however, the *pallipes* female of Say. The *pallipes* male of authors is therefore an unnamed species, for which the author (1940) has proposed the name *Eremobates palpisetulosus*.

It is further evident that the Nebraska series of Solpugida here reported upon is the true *Eremobates pallipes* (Say). The series contains specimens from 25 of Nebraska's 93 counties, the greater number of locality records

coming from the counties in the southern and western parts of the state. Specimens from Lincoln, Lancaster County, Hartington, Cedar County, and Burton, KeyaPaha County, constitute the extreme eastern, northeastern, and northern records, respectively, for the state.

Eremobates pallipes (Say)

Female. (Figs. 2, 3).

Straw colored, the fingers of the mandibles reddish-brown, teeth black, abdomen grayish above, eye tubercle black, malleoli white.

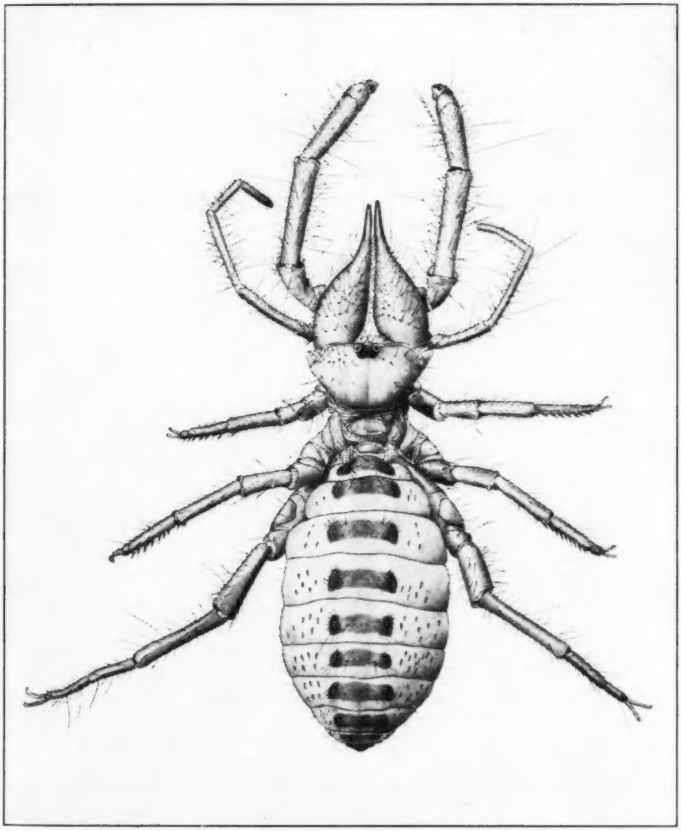

Fig. 2. *Eremobates pallipes* (Say). Female, dorsal view. Drawn from a preserved specimen.

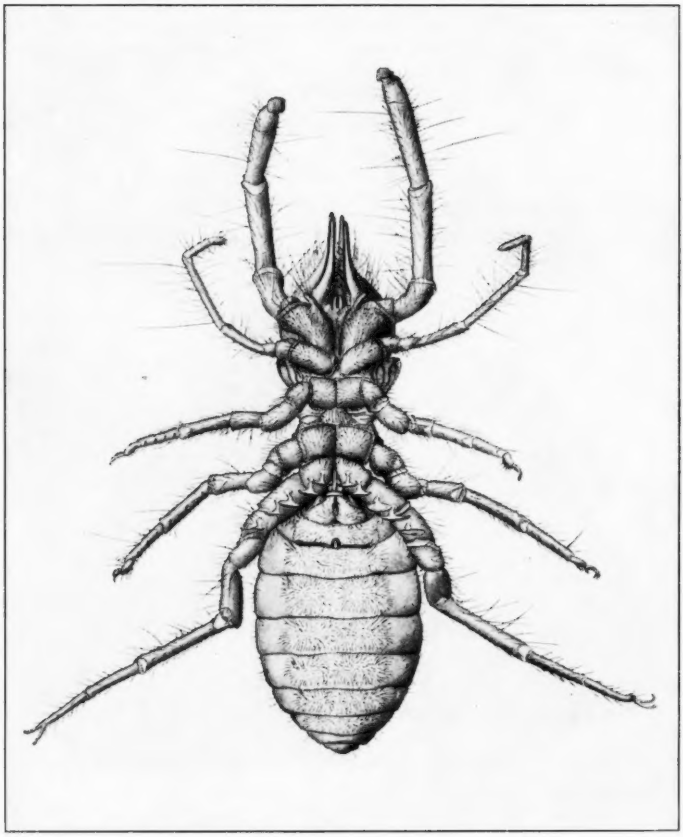

Fig. 3. *Eremobates pallipes* (Say). Female, ventral view.
Drawn from a preserved specimen.

Fixed dorsal finger of mandible about twice the length of the movable ventral finger, and about $^1/_3$ the length of the entire mandible as seen from above. Dorsal finger armed with 3 front teeth of which the 3rd is the largest, the 2nd the smallest; 2 intermediate teeth of which the 2nd is the larger; a single main tooth resembling the 3rd front tooth. Fond with 4 lateral teeth the 1st and 3rd of which are the largest and equal, the 2nd the smallest, and 4 median teeth of which the 1st is much the largest. Between these 2 series of fondal teeth and following the main tooth of the dorsal finger is a row of 4 small teeth only the 1st of which is visible as the mandible is viewed laterally.

Movable ventral finger bears 1 front tooth and 1 main tooth, both large and nearly equal, and between them 2 small intermediate teeth the 2nd of which is the larger and which is set low upon the anterior face of the main tooth. A small tooth medial to the main tooth.

Metatarsus of pedipalp with or without papillae; metatarsus and tibia with many unequal, fine, truncate hairs, fewer on the tibia; long, fine hairs over all of the pedipalp, coarser on the femur, but without true spines.

Tibiae II and III each with a robust dorso-postero-apical spine and 1 or 2 less robust postero-apical spines. Metatarsi II and III each with 5 (or 6, the 2nd weak) robust spines in a dorso-posteriad row which apically tends dorsally, and 4 longer but less robust spines in a posteriad row. (These spines show marked variations in magnitude). No ctenidia.

Body length (range of series) 14-30 mm.

Male. (Fig. 4).

Whitish-yellow, legs paler, fingers of the mandibles and the fond reddish-brown with black teeth, eye tubercle black, the abdomen grayish above.

Fixed dorsal finger and trunk of mandible about twice the length of the movable finger, the dorsal finger about $^1/_3$ the length of the entire mandible as seen from above. Dorsal finger nearly straight, but directed downward from its base upon the trunk. Dorsal finger without teeth. The fond with 4 teeth in the outer or lateral series, the 1st and 3rd being largest, the 2nd the smallest; the median or inner series with 4 teeth, the 1st of which is much the largest, the 2nd and 4th the smallest. Ventral finger as in the female with two large teeth (1 front tooth and 1 main tooth) both directed forward, between which are 2 small teeth, the intermediate teeth, of which the second is the largest, being set low upon the anterior face of the main tooth.

Metatarsus of the pedipalp with the median surface thickly armed with short, truncate bristles; ventro-medially with a scopula of papillae (45 to 75). Pedipalps otherwise adorned with many fine hairs of unequal length.

Tibiae II and III each with 1 robust dorso-postero-apical spine and 1 or 2 rather weak postero-apical spines. Metatarsi II and III each with 5 (or 6, the 2nd weak) robust spines in a dorso-posteriad row which apically tends dorsally, and 4 longer but less robust spines in a posteriad row. (These spine characters questionable because of apparent variations in size of the spines). No ctenidia. Malleoli white.

Body length (range of series) 15-21 mm.

Specimens Examined.—Total 48 (8 ♂, 40 ♀) received from the following Nebraska localities and collectors: Scotts Bluff County—Morrill, 8-30-1937, 1 ♀ (W. A. Batie); Scottsbluff, 7-11-1939, 1 ♀ (E. A. Olson). Box Butte County—Hemingford, 7-6-1939, 1 ♂, 1 ♀ (Edson Fichter); Alliance, 8-2-1937, 1 ♀ (Nat Tolman). Morrill County—Northport, 7-3-1936, 1 ♂ (W. Paine). Cheyenne County—Sidney, 7-17-1937, 1 ♀ (R. D. Hughes); Dalton, 8-12-1938, 1 ♀ (Eunice Mauer). Sheridan County—Rushville,

6-19-1936, 1♀, 6-25-1938, 1♀ (E. M. Huckfeldt), 8-14-1939, 1♀ (C. O. Sawyer); Gordon, 10-15-1936, 1♀ (J. A. Thoroman). Garden County—Oshkosh, 7-11-1936, 2♀, 7-1-1937, 1♀, 9-1-1937, 1♀, 10-19-1937, 1♀ (L. Barnell); Lewellen, 7-30-1937, 1♂, 2♀ (H. A. Blackstone). Keith County—Oglallala, 6-27-1934, 1♀, 7-26-1935, 1♂ (J. W. Hepperly); Roscoe, 10-5-1934, 1♀ (H. J. Chamberlin). Perkins County—Grant, 7-22-1935, 1♀ (T. H. Alexander). Chase County—Champion, 7-18-1932, 1♀ (Bud Pugh); Imperial, 7-15-1939, 1♂ (E. J. Fruhling). Dundy County—Haigler, 7-19-1937, 1♂ (Mrs. J. Havlik). Lincoln County—Brady, 6-20-1939, 1♀ (Lee Anderson), 7-3-1939, 1♂ (Edson Fichter). Hayes County—Hayes Center, 6-24-1936, 1♀ (S. E. Lingo). Hitchcock County—Palisade, 7-24-1937, 1♀ (Bernard Modrell). Logan County—Gandy, 10-1-1934, 1♀ (M. Faulkner). Frontier County—St. Ann, 7-29-1939, 2♀ (John Wasia). Blaine County—Purdum, 8-12-1938, 1♀ (F. W.

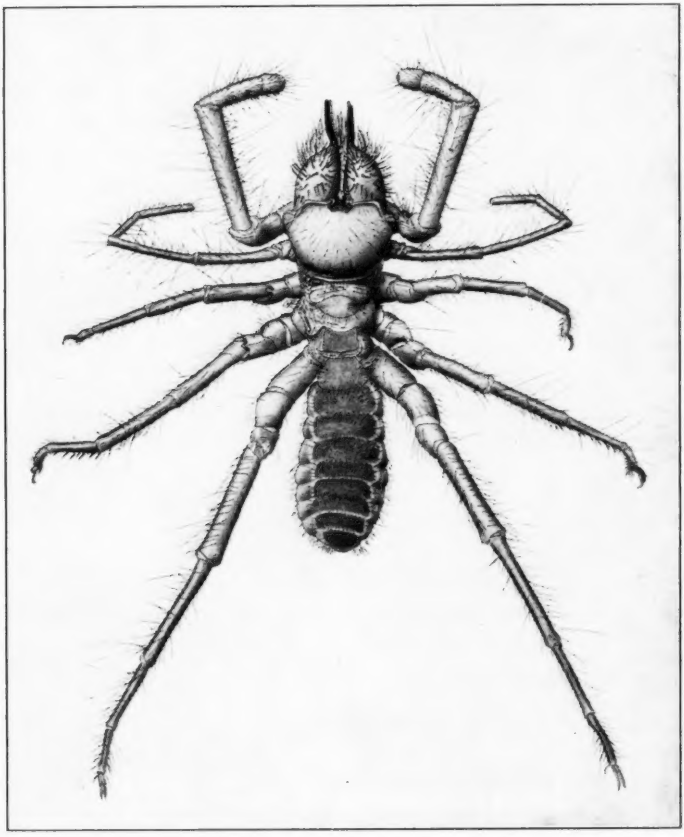

Fig. 4. *Eremobates pallipes* (Say). Male, dorsal view. Drawn from a preserved specimen.

Body). KeyaPaha County—Burton, 7-7-1937, 1 ♂ (E. E. Ritterbush). Dawson County —Lexington, 8-18-1932, 1 ♀ (James C. Adams). Gosper County—Elwood, 8-14-1937, 1 ♀ (D. C. Joy), 7-23-1939, 1 ♀ (Byron D. Sadle). Furnas County—Oxford, 7-14-1936, 1 ♀ (M. Brown), 6-28-1937, 1 ♀ (Duryee Drug Co.), 7-15-1937, 1 ♀ (Mrs. C. Shumaker). Harlan County—Huntley, 9-26-1938, 1 ♀ (Doris Gates). Howard County—St. Paul, 8-2-1937, 1 ♀ (A. W. Krueger). Thayer County—Alexandria, 7-19-1939, 1 ♀. Cedar County—Hartington, 8-3-1939, 1 ♀ (J. C. Rosse). Lancaster County—Lincoln, 6-4-1938, 2 ♀ (Edson Fichter).

An apparently domiciliary tendency on the part of *Eremobates pallipes* has probably been in considerable measure responsible for the receipt of many of the specimens from correspondents. Thirteen specimens have been reported as found in houses, 3 of these 13 "in beds."

The writer has collected 7 specimens of *Eremobates pallipes* in a period of two years. All of these have been found in dry situations. Four female specimens were taken on the steep southwest slope of a sandstone hill south of Lincoln, Lancaster County, Nebraska. They were found under stones, where they had excavated for themselves shallow burrows in the sandy soil produced by the weathering of the outcropped sandstone. Another female was collected in the loess hills south of Brady, Lincoln County, Nebraska. It was beneath a cow chip on the nearly level floor of a ravine. Two specimens, a male and female, taken near Hemingford, Box Butte County, Nebraska, were found beneath cow chips in overgrazed range country.

In all cases the individuals collected have been found alone. Two of the females collected at Lincoln were placed together in a vivarium measuring about 2 by 4 inches of floor space. The following morning only one individual remained, the mangled portions of the exoskeleton of the other specimen bearing mute evidence of cannibalism.

The other two females taken at Lincoln were kept in separate vivaria from the date of collection, June 4, 1938, until their deaths, August 13 and 17, 1938, respectively. At death the abdomens of these females appeared greatly distended with eggs, each extruding a few eggs shortly before dying. A female with the collection date of July 11, 1936, taken at Oshkosh, Garden County, appears to have been gravid at the time of collection.

The specimens kept in vivaria during the summer of 1938 were fed grasshopper nymphs. The prey is evidently located by contact, the pedipalps being particularly functional in this respect. The attack on the grasshopper is markedly sudden, and, if successfully executed, is immediately followed by the chewing action. This chewing, which continues throughout the entire feeding, is accomplished as follows: The vertically operating fingers of the chelicerae work one set at a time, i. e., first the right and then the left, only the lower finger of each chelicera moving, and with moderate speed. At no time during feeding was a specimen observed to open and close both jaws simultaneously. The body of the insect is slowly mutilated. Mangled pieces of exoskeleton are worked through the jaws from one side to the other, the soft parts of the insect being ingested, the hard chitinous portions, which tend to remain together,

rejected. When the arachnid is finished with the grasshopper the latter is a shapeless mass. The alimentary canal, at least in the abdomen where it is more easily observed, is not eaten. Throughout the feeding act the abdomen of the arachnid is pumped or contracted spasmodically at intervals of from 3 to 7 seconds. This region of the body is noticeably distended after feeding.

When water was dropped into the vivarium so as to splash from a flat stone which rested on the surface of the sand, a specimen of *E. pallipes* would turn to face the splashing and advance toward it, following which it would drink from standing droplets of water.

When burrowing, the first pair of walking legs (legs II) is used in clawing the loose sand backward under the abdomen. When a large piece of gravel is encountered it is taken in the chelicerae; the solpugid backs up, drops the stone, and walks over it in returning to the excavation. When a small pile of sand has been pushed up under the abdomen she turns around, opens the chelicerae widely, and pushes the pile along with the open chelicerae, keeping the sand from spreading from the sides of the pile with the pedipalps and legs I.

The captive females of *E. pallipes* were often noted climbing the sides of the battery jars which served as vivaria. This was accomplished solely by the use of the suction organs at the tips of the pedipalps.

Many of the above observations upon *E. pallipes* are closely comparable with certain of those reported or quoted by Turner (1916) concerning this and other species of American Solpugida.

The writer wishes to express his gratitude for the help and guidance of Prof. Myron H. Swenk of the Department of Entomology, University of Nebraska, who suggested this study and under whose direction it has been pursued.

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On the Occurrence of Water Mites in the Food of Turtles

Ruth Marshall

The Hydracarina of the present collection were found by Mr. Karl F. Lagler, of the University of Michigan, in the course of his investigations on the food and habits of the common turtles of Michigan and kindly given to the author for examination. In letters and manuscript (unpublished) Mr. Lagler states that he examined the contents of the digestive organs of 965 turtles belonging to seven species captured in the summers of 1937 and 1938 in several lakes of the Southern Peninsula. Of these, only two species, the western painted turtle *(Chrysemys picta marginata)* and the snapping turtle *(Chelydra serpentina)*, had swallowed water mites which were recovered; there were six individuals of the first species and forty-four of the latter. Consequently water mites cannot be considered of any importance as turtle food; they were found almost invariably associated with algae and were doubtless taken incidentally in feeding. It may be noted that the digestive juices of these turtles had little effect on the water mites, even when they were recovered near the end of the tract. This is in contrast to the effect observed on specimens recovered from the digestive tracts of fishes where there was much disintegration. (Marshall, Water Mites from Wyoming as Fish Food. Trans. A.M.S., 1933, 52:34). In addition to the turtle material, one individual (to be described later) was found in the stomach of the great blue heron *(Ardea herodias)*.

However, as the first record of Hydracarina recovered from turtle food, as far as the author is aware, this collection has some interest. More than 200 individuals were found, representing nine genera and thirty-five species and varieties; several *Arrenurus* females and a few *Piona* nymphs were not identified. Of special interest was the finding of the previously unknown females of two rare species; these will be next described and then the complete list of the species added.

Limnesia wawaseea Mar.

Fig. 1

In the food mass of a snapping turtle from Ferguson Lake there was found one individual belonging to the subgenus *Tetralimnesia* and identified as the hitherto unknown female of *L. wawaseea,* the only representative of the subgenus so far described for North America. Accurate measurements could not be made, since the specimen is young and somewhat distorted from its contact with the digesting food; it is smaller than the two old males (2.73 mm.) of the original description (Marshall, Proc. Indiana Acad. Sci.,

1929, 38:315), the only specimens so far reported. The body surface is covered with very fine points which appear to coalese in the mature individuals. The epimera (here close together), show the same details as in the male; most characteristic is the medial margin of the first pair where there is developed a short horizontal chitin bar. The broad genital plates, slightly bulging in the region of the third acetabula, show the characteristic four acetabula each, of which the second is slightly the smallest and is a little more separated from the third than from the first. These plates are distinguished also by the presence of a large number of fine hairs with their supports, most of them very short, grouped irregularly around the acetabula; the number found in this individual female was not as great as in the males, a difference which may be due to age or to sex.

Hygrobates multiporus Koen.

Fig. 2, 3

One individual of this rare species was found in the stomach of a great blue heron secured near Marquette, Mich., May 11, 1936. The species was incompletely described by F. Koenike (Abh. natur. Ver. Bremen, 1895, 13(2):216) with one drawing (the genital plates), from the examination of a single individual, a male, not in good condition, found in British Columbia. The author has seen this specimen, poorly preserved on a slide, and lacking the palpi. However, the distinctive character of the genital plates, with several small acetabula instead of the six large ones common for the genus, together with the partial description, makes identification certain. The new individual is a female, in good condition; hence the original description can now be completed.

The body of *Hygrobates multiporus,* female, is oval, slightly indented between the eyes, 1.60 mm. long, 1.35 mm. wide (Koenike gave "etwa 1 mm" for the male). The body surface is heavy, dark, and no color was preserved. The delicate cuticula is finely lined. There are short antennaty bristles. Many eggs were found in the body. The epimera lie in the anterior third of the body; the first pair, partially fused with each other and the maxillary organ, are relatively broad posteriorly, while the fourth are roughly rectangular. The genital plates, situated just below the center of the ventral surface, show the character which suggested the specific name: on one plate were found eleven acetabula, on the other, eight, varying considerably in size (Koenike found nine and eleven for the male). Many fine hairs were found among the acetabula. No description of the palpus was given by Koenike; it is shown in the present paper in fig. 2. It is a little wider than the legs and bears several heavy bristles; the cone on the flexor side of the 2nd segment is moderately developed and sparsely covered with denticles, as is also the same surface on the 3rd. The 4th palpal segment bears two fine hairs on minute papillae midway on the flexor side, wihile the fifth ends in two finger-like processes. The legs are sparsely provided with heavy bristles but no swimming hairs.

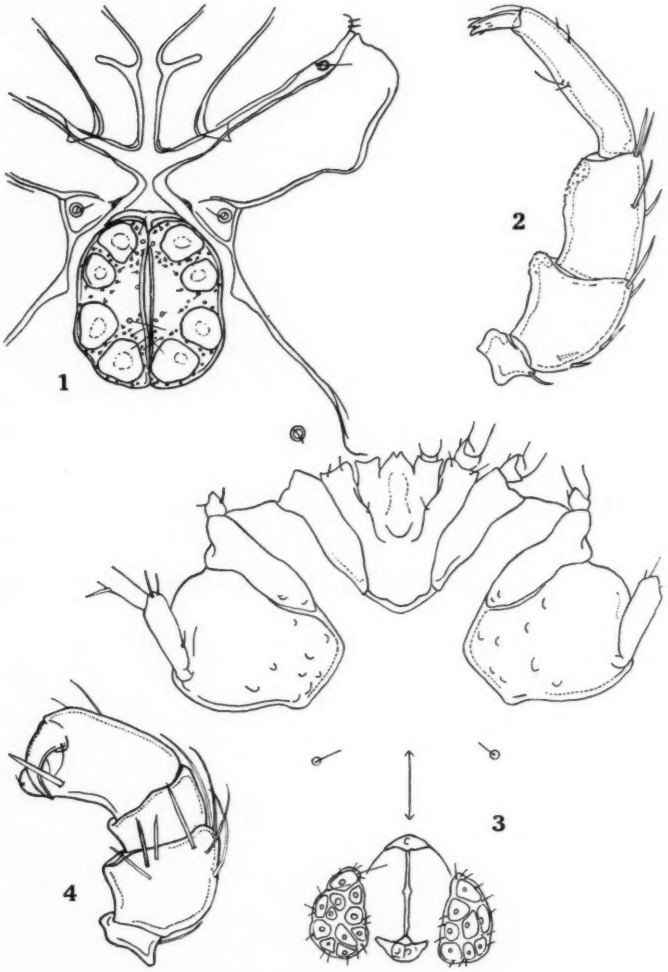

Fig. 1. *Limnesia wawaseca*, genital area, female.
Fig. 2. *Hygrobates multiporus*, right palpus, female.
Fig. 3. *Hygrobates multiporus*, ventral plates, female.
Fig. 4. *Arrenurus amplus*, right palpus.

List of Species

1. *Diplodontus despiciens* (Müll.)
2. *Oxus connatus* Mar.
3. *Frontipoda americana* Mar.
4. *Limnesia undulata* (Müll.)
5. *wawaseea* Mar.
6. *Hygrobates multiporus* Koen.
7. *Unionicola crassipes* (Müll.)
8. *Neumania semicircularis* Mar.
9. *punctata* Mar.
10. *tenuipalpis* Mar.
11. *armata* Mar.
12. *ovata* Mar.
13. *distincta* Mar.
14. *Koenikea concava* Wol.
15. *wolcotti* Viets
16. *Piona reighardi* (Wol.)
17. *exilis* (Wol.)
18. *pugilis* (Wol.)
19. *spinulosa* (Wol.)
20. *wolcotti* Mar.
21. *Forelia liliacea* (Müll.)
22. *Mideopsis orbicularis* (Müll.)
23. *Krendowskia similis* Viets
24. *Arrenurus crenellatus* Mar.
25. *infundibularis* Mar.
26. *scutulatus* Mar.
27. *manubriator* Mar.
28. *marshallae* Piers.
29. *megalurus* Mar.
30. *intermedius* Mar.
31. *pseudocylindratus* Piers.
32. *wardi* Mar.
33. *laticornis* Mar.
34. *falcicornis* Mar.
35. *amplus* Mar.

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Ostracoda from Beaufort, North Carolina Sand Beaches

Willis L. Tressler

The material reported upon in this paper was collected during the summer of 1939 by Dr. A. S. Pearse, Dr. George Wharton and Miss Helen Ramsay. The Ostracoda were separated from the sand and from other organisms and sent to the writer for identification. Collections were made at various places on flats, in intertidal zones and at low tide mark on several beaches near Beaufort between June 13 and August 25, 1939. Small amounts of sand were collected in salve boxes about 5 cm. in diameter and the contained organisms in the sand were then sifted out and preserved; all were living at the time of capture.

The total number of ostracods examined was 128 which were included in eight species belonging to six genera. All belonged to the family Cytheridae. Some of the specimens were either immature or were larval stages and could not be identified with certainty. All of the species identified have been found in littoral or near-littoral zones elsewhere and many of them are known to be inhabitants of very shallow water among algae. The ostracods in the Beaufort sands in all probability do not belong to the regular fauna which exists among the sand grains as reported by Pennak (1939). These ostracods, while extremely small, are too large to exist between sand grains and probably were left stranded by the tide or were found resting on the sand when samples were taken in shallow water. The family Cytheridae, to which all the forms belong, is composed of strictly bottom dwelling ostracods which possess no power of swimming.

In the following account I shall follow the classification and synonymy of G. O. Sars (1928), which differs somewhat from that established by Müller (1912).

Family CYTHERIDAE

Subfamily CYTHERIDEINAE

Genus *Cytheridea* Bosquet

1. *Cytheridea papillosa* Bosquet

Occurrence.—Seven individuals of this easily recognizable species were taken from two localities: Sheepshead Shoal, flats, July 25; Sheepshead Shoal, tide pool, August 3.

Distribution.—This ostracod has previously been taken only in more northern regions. It has been found at moderate depths off the coast of Norway, the British Isles, Iceland, Greenland, Spitzbergen, Gulf of St. Lawrence, Franz Joseph Island and in Vineyard Sound off the Massachusetts coast.

2. *Cytheridea rubra* G. W. Müller

Occurrence.—This species was the most numerous and widely distributed of the ostracods found on the Beaufort beaches. Thirty-nine specimens were taken from seven localities: Sheepshead Shoal, intertidal zone, June 13, July 25, July 27, August 16; Sheepshead Shoal, tide pools, July 25, July 27; Sheepshead Shoal, flats, June 22, July 25, August 22, August 25; Shipstake Shoal, flats, June 20; Bird Shoal, flats, June 20; Guthrie Shoal, one foot under water, June 27, August 9; Ft. Macon Beach, inside, low tide mark, July 10.

Distribution.—This ostracod has been found in the zone between sand and seaweeds in the Gulf of Naples and in Vineyard Sound on the North American coast.

Subfamily CYTHERINAE

Genus *Cythere* O. Fr. Müller

3. *Cythere viridis* O. Fr. Müller

Occurrence.—Seven individuals of this species were collected from five localities: Sheepshead Shoal, tide pool and from the flats, July 25; Sheepshead Shoal, tide pool, August 3; Guthrie Shoal, one foot under water, August 9; Sheepshead Shoal, intertidal zone, August 17.

Distribution.—This octracod has been found close to the beach among algae along the Norwegian coast and has also been taken along the British coast and in the Kattegat.

4. *Cythere albomaculata* Baird

Occurrence.—Only four specimens of this form were taken at two localities: Sheepshead Shoal, intertidal zone, June 13; Ft. Macon Beach, outside, 3.5 meters deep, June 19.

Distribution.—This species occurs in the laminarian zone off the coast of Norway, the British Isles, Iceland, Bay of Biscay and has been collected off the Bureau of Fisheries dock at Woods Hole, Massachusetts.

Genus *Xenocythere* G. O. Sars

5. *Xenocythere cuneiformis* Brady

Occurrence.—Five specimens of this ostracod were collected at two localities: Sheepshead Shoal, tide pool, August 3; Sheepshead Shoal, intertidal zone, August 17.

Distribution.—This form occurs at moderate depths off the coasts of Norway and the British Isles.

Subfamily CYTHERURINAE

Genus *Cytherura* G. O. Sars

6. *Cytherura striata* G. O. Sars

Occurrence.—This species was widely distributed; twenty specimens were

taken from six localities: Sheepshead Shoal, intertidal zone, July 25, July 27, August 17; Sheepshead Shoal, flats, August 21, August 22; Sheephead Shoal, low tide mark, July 27; Sheepshead Shoal, 0.5 meters below low tide mark, August 7; Bird Shoal, flats, June 20; Ft. Macon Beach, inside, low tide mark, July 10.

Distribution.—This species is found off the Norwegian coast at depths of between 10 and 20 fathoms. It is also found off the coasts of Holland and the British Isles and in the Mediterranean.

Subfamily XESTOLEBERINAE

Genus *Xestoleberis* G. O. Sars

7. *Xestoleberis aurantia* (?) (Baird)

Occurrence.—Seven specimens were taken from three localities: Sheepshead Shoal, intertidal zone, July 25; Sheepshead Shoal, tide pool, July 25; Guthrie Shoal, one foot deep, June 27. All the specimens were immature.

Distribution.—This ostracod is a distinctly littoral form, being found along the Norwegian coast close to the beach, among algae. It is also found on the coast of the British Isles, in the Baltic, the Kattegat and on the coast of Holland. The closely allied species *Xestoleberis depressa* has been taken in Vineyard Sound on the Massachusetts coast.

Subfamily PARADOXSTOMINAE

Genus *Cytherois* G. W. Müller

8. *Cytherois pusilla* G. O. Sars

Occurrence.—This was the most abundant species, excepting *Cytheridea rubra,* 23 specimens being collected from three localities: Sheepshead Shoal, intertidal zone, July 25, July 27, August 17; Sheepshead Shoal, flats, July 25, August 22; Sheepshead Shoal, tide pool, July 25, July 27.

Distribution.—This form has been found in shallow water among algae off the Norwegian coast.

DISCUSSION

It is astonishing how little work has been done on the marine Ostracoda of the Eastern North American coast, particularly along our own shoreline. As a result, the Ostracoda of this region are almost entirely unknown and indeed, as far as the writer has been able to determine, Cushman's report on the Ostracoda of Vineyard Sound and adjacent waters (Cushman, 1906) still remains the sole attempt at a contribution to the knowledge of our littoral marine species. If one travels farther north to the Gulf of St. Lawrence and into the Arctic one finds, surprisingly enough, that more is known of the Ostracoda of these less accessible regions than of our own shores but even here the surface has barely been scratched as far as a complete knowledge of the distribution of these little animals is concerned. Cushman (1906) quotes

Brady and Norman (1889) as follows: '"The Ostracoda of the American side of the Atlantic have not been studied, and our endeavors to procure material from that portion of the area have hitherto failed. A few species from the Gulf of St. Lawrence were described some years ago by Dr. Brady, but nothing whatever is known of the species which inhabit the coasts of the United States."' Cushman made the following comment: "This was written over fifteen years ago but the same condition of things still prevails." In his paper on the Ostracods of Vineyard Sound, Cushman reports on twenty-six species belonging to eleven genera. It has now been thirty-four years since Cushman's paper and still nothing further has been made known concerning the distribution of marine Ostracoda along our eastern coast.

The species found in the Beaufort sands are mainly forms which occur in much more northern latitudes in Europe and many of them are distinctly northern forms in other parts of the world. *Cytheridea rubra* was first found in the Mediterranean and is an exception to the above. Cushman (1906) found this ostracod to be present off the coast of Massachusetts and in addition found *Cythere albomaculata* and *Cytheridea papillosa*. He believed that many of the forms which he found in Vineyard Sound were Arctic forms which were near their southern limit in the cold waters of Vineyard Sound. The finding of some of these species as far south as North Carolina greatly extends their known southern limit and may indicate that the distribution of some of them, at any rate, is still imperfectly known.

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Ecological Observations on the Common Mollusks of Sanibel Island, Florida

Fritz Haas

The environmental factors affecting marine molluscan life are so numerous and so varied that adequate study is possible only when a restricted area is selected. There are some published descriptions of the effect of storms on the molluscan fauna of marine beaches, and of the obviously important role of mollusks in the formation of such beaches. The normal beach life, the immediate effect of a storm upon it, and the gradual return to normal conditions at Sanibel Island in June of 1939 seemed to me to be especially interesting and worthy of record.

An opportunity to study a characteristically developed shell beach was provided in 1939 when the author visited Sanibel Island, Florida, as a member of the Florida Expedition of Field Museum. Although time and facilities were limited, the cooperation of several local people made possible a highly interesting series of observations on the ecology of the molluscan fauna of this region. It is a pleasure to the author to express his sincere gratitude to Mrs. L. M. Perry and Mrs. F. R. Schwengel for the use of their collecting apparatus; to Messrs. G. J. Kessen and George Underhill for their advice and suggestions regarding local natural history; and to the Matthews family for providing laboratory and other technical facilities in Island Inn.

Physical Features of Sanibel Island

Sanibel is the largest and most southerly of the series of islands extending southward from the mouth of Charlotte Harbor, on the Gulf side of the Florida peninsula. Sanibel Island itself lies at about latitude 26° N and longitude 82° 5′ W, opposite the mouth of the Caloosahatchee River, four to six miles from the adjacent mainland. It measures about twelve miles in length and from three fourths of a mile to three miles in breadth. Geographically the island is subtropical, but biologically it is frankly tropical as a result of the warm Gulf waters that wash its shores, as is recognized in Merriam's assignment of this part of Florida to the "Tropical Life Zone."

The whole of Sanibel is literally composed of shell deposits almost eighteen feet deep, which presumably rest on a coral reef base. Breaking up of innumerable millions of shells, their reduction to fragments, and finally to shell sand, is rapidly going on in the intertidal belt. Above that belt more shells have been piled up on the shore by the action of storms. The beach represents a vast mortuary. No sorting according to size or to the convexity of the valves could be found in these densely packed deposits. About 99.9% of these littoral deposits are composed of mussel shells, with shells of gasteropods making up the other 0.1%.

The littoral vegetation is dominated by the cocoanut palm, the beach morning glory *(Ipomoea pes-caprae)*, the beach grape tree *(Coccoloba uvifera)*, the black mangrove *(Avicennia nitida)*, and the red mangrove *(Rhizophora mangle)*. The central part of the island is largely given over to introduced trees, such as papaya, mango, lime, and guava, although two indigenous species of figs (*Ficus* spp.) are common. The westward side of Sanibel, facing the open Gulf of Mexico, is a bare sea beach. The landward side presents more varied conditions, differing especially in the presence of mangrove-filled inlets. The discussion below will contrast the conditions of life for the marine mollusks on the two sides of the island. The molluscan composition of the deposits on the Gulf side throws light on the paleobiological problems presented by beach deposits of past geological ages.

Fragments of a mussel brecchia, called "coquina" in Sanibel, are to be found on the beach, and even below water at a point on the Northwest coast. The "Rocks," off the Gulf coast, at about one and a half mile from the NW point of the island, are composed of coquina. This coquina is a loosely consolidated rock composed of more or less broken and worn shell fragments. The pieces of this rock on the beach are from a layer an inch or more in thickness. The Sanibel beach seems in fact to be a favorable locality to study the origin of such limestones.

Composition of the Normal Beach

The coast on the Gulf side of the island slopes down very gently. Charts indicate a depth of only about twenty feet four miles off shore, and the dredge net brings up a bottom of drifting sand at this depth. Lack of stones or rocks on the bottom is further indicated by the fact that sponges, which in turn have encouraged other sessile animals, have settled on fragments of *Pinna* shells and on the mytilid *Brachidontes exustus*, sometimes entirely concealing the shell.

Shallow water fauna.—Approximately 120 species of bivalves are known from the Sanibel fauna. Very few of these are really rare, but seven species make up the great majority brought up in the dredge net. These are, in order of frequency, first *Arca ponderosa* Say; then in almost equal numbers *A. secticostata* Reeve and *A. transversa* Say; next, *A. occidentalis* Philippi, *Pinna rigida* Dillwyn, *Brachidontes exustus* Linnaeus, and *Pecten gibbus gibbus* Linnaeus.

Intertidal zone.—Normally the surf-beaten intertidal zone of the Sanibel beach is practically devoid of living mollusks. This is due to the fact that the action of the surf renders creeping or digging almost impossible; animals that cannot dig themselves very deeply into the sand during low tide are whirled around and thrown out. It is in the intertidal zone that the shells deposited on the beach by storms are ground and pulverized, with the result that most of the beach sand is composed of triturated shell matter.

The only mollusk that succeeds in establishing itself in this rough zone is *Donax variabilis* Say. When torn out of the bottom by a wave, this small

bivalve buries itself again with astounding quickness before the next wave arrives. This continues until the receding sea offers the animal a chance to rest. The sand bug (*Hippa talpoida* Say), an anomurous crustacean, is at home in the todal pools behind the low water bar, and in the intertidal zone in general, swimming briskly around at high tide and hiding in the sand when the tide is out.

Supratidal zone.—In the packed and stratified shell deposits above high water, in which each stratum corresponds to a separate storm, all the shells are in a perfect state of preservation, but not glued together. Mussel shells compose about 99.9% of the littoral deposits above the tidal zone, with only 0.1% of gasteropods. This small percentage of gasteropods includes only seven species (out of about 250 species in the Sanibel fauna), in order of frequency as follows: *Crepidula fornicata* Linnaeus, *Pyrula papyracea* Say, *Strombus pugilis* Linnaeus, *Busycon perversum* Linnaeus, *B. pyrum* Dillwyn, *Fasciolaria gigantea* Kiener, and *Oliva litterata* Say. The relatively high frequency of *Crepidula fornicata* is due to the fact that its shell is flat and mussel-like. The shells of *Pyrula papyracea* are mostly broken.

Of the bivalve shells, comprising the remaining 99.9% of the shells, at least 95% are arcas; *Arca ponderosa* in superabundance, followed by *A. secticostata, A. transversa,* and *A. occidentalis.* Although the shells of the latter three forms are by no means rare, they are not easily found in the shell deposits because they are quite lost among the much more prevalent *Arca ponderosa.* The reason for their low frequency is probably due to the fact that the structure of their shells does not facilitate their transportation by the waves, *secticostata* being heavier, while *transversa* and *occidentalis* do not present the optimal degree of convexity as *ponderosa* apparently does. The next obvious component of this beach material above the tidal belt is *Pinna rigida* Dillwyn, which apparently can be easily transported by the waves, its shells being light and adequately convex. The arcas and pinnas constitute about 95% of the whole beach material in question.

There is evidence that even living pinnas can be washed up on shore. A festoon of cast-up material, about fifteen and one half miles long and, on the average, one and a half feet wide, which paralleled the entire Gulf shore of Sanibel Island and which had been piled up after a storm, was composed almost entirely of *Pinna* shells; at the NW corner of the island, this festoon was occasionally twelve to fifteen feet wide and about seven inches deep, densely packed, and almost pavement like. An estimate based on the occurrence of about seventeen *Pinna* shells in each foot of this festoon suggests a total of about 1,000,000 shells! The annihilation of about a million individuals of a single species by a single storm on a beach only about fifteen and a half miles in length apparently did not appreciably affect the density of population of *Pinna* in the shallow water along the beach. The *Pinna* valves in the great windrow of shells were still connected. No odd valves were found, and the internal faces of the shells were free from sessile animals, which proves that the shells, at the time of the accident, must still have been inhabited by the

living animal. The windrow of *Pinna* shells was composed of about 98% of *Pinna rigida* and 2% of *Pinna serrata* Sowerby.

The four species of *Arca* and the two of *Pinna* we have enumerated form about 98% of the total littoral deposits; the composition of the remaining 1.9% of the bivalve material still remains to be explained. The components of this remainder are:

Pecten gibbus gibbus Linnaeus	*Beguina floridana* Conrad
Anomia simplex Orbigny	*Cardium robustum* Solander
Pteria colymbus Bolten	*Spisula solidissima similis* Say
Venus mercenaria notata Say	*Chione cancellata* Linnaeus

Only a vanishingly small percentage is constituted by other species, which, though by no means very rare, are lost among the immense number of the more common species. It is surprising that the beach bivalve *Donax variabilis* which can be taken by the thousands in the intertidal belt, does not appear at all in the littoral deposits. *Pteria colymbus* and *Cardium robustum* occur frequently with connected valves. In shells in which the right and left valves offer a different degree of convexity (*Pecten, Anomia,* etc.), the more convex valve is decidedly more abundant in the beach material than the flatter one.

The Beach after a Storm

The normal aspect of the Gulf beach on Sanibel Island in both the intertidal and supratidal zones is greatly changed after heavy storms from the Gulf, and especially after one of the dreadful hurricanes which attain a velocity of more than eighty miles an hour. These storms disturb the water to a depth of about thirty feet, and the waves wash the animals and plants torn loose from the ocean floor onto the shore. Even species of mollusks normally not to be found on the beach are thus thrown up. Such forms include the rare volutid *Maculopeplum junonia* Chemnitz, *Cypraea exanthema* Linnaeus, *Conus proteus* Linnaeus, and the bivalves *Tellina radiata* Linnaeus, *T. alternata* Say, and *Lyonsia floridana* Conrad; they may be collected alive or recently dead, when such a storm is over.

During my stay on Sanibel Island, I witnessed the relatively light storm of June 12-15, 1939, which attained not more than about thirty-five miles an hour at its maximum. This gave me an opportunity to observe the changes thus caused in the beach deposits. When the waves had calmed somewhat and the newly built-up shell deposits, which corresponded to the maximum height of the storm flood, were laid bare, the unusually large number of animals quite new to the beach, and especially of gasteropod shells, became obvious. Many *Strombus pugilis* had been thrown ashore from the calm depths where they generally live. Those that had not yet died from desiccation were trying to protect themselves from the action of the waves, to which they are unaccustomed, by burrowing in the sand; but most of them perished within a few days by being buried and subsequently suffocated in the sands; from day to day fewer living ones and more dead ones were found on the beach. Living young *Fasciolaria distans* Lamarck were found in the intertidal zone, and their be-

havior and fate paralleled the case of *Strombus pugilis*. Several species of muricid gasteropods, unfit either to withstand the action of the surf or to escape this zone, face the same destiny. *Crepidula fornicata,* whose chains, settled on mussel shells, are thrown up on the beach, perish even more quickly, since the animal does not move and cannot escape in any way.

The bivalves washed up by the storm suffer the same fate as the gasteropods. The vast majority of mussels washed ashore consists of the most common species, *Arca ponderosa;* but it is chiefly small specimens, up to three quarters grown, that are thrown up. This species dies in thousands by desiccation, in the deposits above the high-water level. In the intertidal zone it attempts to escape the effect of the surf by burying itself in the sand; but since every oncoming wave throws it up again, it generally ends by being buried and choked. That adult *Arca ponderosa* are rare among the victims of the storm is probably due to their sticking deeper in the sea floor than the younger ones, so that even the rough water cannot throw them out. The three rarer species of *Arca, secticostata, transversa,* and *occidentalis,* behave in quite the same manner as *Arca ponderosa.*

Pinctada radiata Lamarck, *Pteria colymbus, Modiolus tulipa* Linnaeus and *Brachidontes exustus,* all light shells, moored to some foreign body by byssus threads, can frequently be found living or dying on the beach after a storm. They are of special interest as they generally are washed ashore with the base on which they have settled. In most cases this base is a valve of a mussel, usually an *Arca,* resting on the ocean floor on its concave surface and settled on the convex surface by a gorgonid, a hydrozoan, or some other object, on which, in turn, these bivalves have anchored themselves. The only other bivalve thrown ashore alive is *Pinna rigida,* mostly as half-grown specimen.

There are surprisingly few echinoderms and tunicates among the victims of storms on Sanibel Island, but a few sponges are common on the beach after a storm. Hermit crabs with their shells, and dromiid crabs of the genus *Hypoconcha* (Guérin), which inhabit odd mussel valves, are rather frequent after a heavy gale, but begin to disappear very soon, either because they return to calmer depths or because they have been killed by the surf or by the many herons and terns which watch the seashore for food.

The Gulf beach of Sanibel Island, normally almost destitute of living animals, is overcrowded with animal life the first days after a storm, mostly by gasteropods and bivalves washed up from greater depths of the sea. All the specimens thrown ashore by the waves at the highest point of the storm lie above the normal high-water mark and die from lack of water, or become the victims of predators like herons, pelicans, cormorants, terns and raccoons. The mollusks deposited within the intertidal belt have a chance of surviving for a short period. Those that are able to retire into the tidal pools behind the low-water mass themselves in these sheltered basins to the degree of literally paving the floor. Such gasteropods and bivalves as are able to bury themselves in the sand hide there during low tide, and thus escape the suction of the receding water. But bivalves unable to make use of the foot, like *Pinctada, Pteria, Pinna,* and the mytilids, are caught by the waves, and continue floating

in the water from high tide to low tide and from low tide back to high tide; they knock against each other so that their shells grit audibly, thep smash each other and expose the animals thus bared to inevitable death, usually by suffocation in sand. These dead or dying *pinnas*, which constitute such a high percentage of the beach deposits, finally come to rest below high-water mark, and the odor of putrefaction is soon perceivable at a great distance. The tiny crabs of the genus *Pinnotheres*, commensals of the pinnas, desert their dying shell host and roam and swim uneasily in the surf zone, where they are also destined soon to perish.

These victims of the storm floor that find a temporary asylum in the tidal pools, and are able to creep and bury themselves, are:

Bivalves	Gasteropods
Arca ponderosa Say	*Strombus pugilis* Linnaeus
Arca transversa Say	*Murex* spp.
Chione cancellata Linnaeus	*Fasciolaris distans* Lamarck
Venus mercenaria notata Say	*Fasciolaris tulipa* Linnaeus
Venus campechiensis Gmelin	*Fasciolaris gigantea* Kiener
	Buscyon spp.

All these mollusks try to find shelter in the sand before the receding flood at low tide can tear them out, and it is a strange sight to see the gasteropods burying themselves with the points of their shells directed downward. When the residual pools that communicate with the open water have emptied at low tide, occasional movements of the floor or jets of water rising from the bottom betray the presence of a rich fauna hidden under the sand while the tide is out. When the tide returns, it either covers the still-buried animals with sand and consequently chokes them, or the waves team them out and whirl them around again until they are killed. The fresh, empty shells of the bivalves and those of the gasteropods containing the dead remains of the animal become more common every day, and the number of the living animals in the pools diminishes correspondingly. The beach, overcrowded for a short time, is soon again a mortuary. The grinding action of the surf at once begins on the shells of these mollusks. The waves tear off their ligaments, polish their outer surface, grind the valves by mutual friction, and finally break them up. After a short time the beach has regained its usual aspect, revealing only worn and polished mussel valves, with practically no gasteropod shells.

The Molluscan Fauna of the Bay Coast

Let us leave the Gulf coast of Sanibel and turn to the shore opposite the mainland, which may be called the Bay coast. The narrow, shallow sound that separates Sanibel Island from the Mainland of Florida is called Pine Island Sound in the north and San Carlos Bay in the south; its width is between four and six miles, and its depth varies from sixteen to eighteen feet, occasionally even twenty feet, its average scarcely exceeding six feet. Its water is scarcely at all brackish at the Sanibel coast, though Peace River, the Calloosahatchee, and the Myakka, discharge into it. The depths below about five feet present a bottom consisting of fine shell fragments and sheltering only a poor fauna.

The common species found here, both alive and dead, are *Arca transversa, Leda acuta* Conrad, *Megaxinus floridanus* Conrad, and *Chione cancellata.* Other species of the Gulf coast, and especially the gasteropods, also occur on the Bay coast, but are rare. The shallows of San Carlos Bay, which are almost bared at low tide, are rather densely covered by the eel grass, *Zostera marina* Linnaeus. The bottom in these shallows is usually sandy, or has a thin layer of mud over the sand. Such places are characterized by the presence of *Pinna rigida, Pecten gibbus dislocatus* Say, and *Venus campechienss.*

Shallow spots that are wholly uncovered at low tide have a sandy bottom, destitute of vegetation; the lucinid bivalve, *Megaxinus floridanus,* characterizes them. Several places in the sound between Sanibel Island and the mainland, which present a harder bottom of coquina or dead coral reef, are settled by oysters, probably *Ostrea virginica* Gmelin, forming real oyster reefs; the species in question is the only one found in San Carlos Bay and in Pine Island Sound, and does not live on the Gulf coast of the island. In most cases the two species of mangrove are associated with these oyster colonies, and masses of mangrove contribute to the enlargement of the reefs by providing additional space for individual oysters as well as by retaining sediment between the roots; the small islets thus originated are inhabited by pelicans, cormorants, various species of herons, and by mosquitoes, all of which find favorable life conditions.

The San Carlos Boy coast of Sanibel is indented by narrow inlets reaching far into the body of the island; a thick vegetation of mangrove covers their margins, and it is bordered on its outer sides by shallows and sand flats, barren, if bared at low tide, and covered with eel grass, if not exposed. The fauna of these shallows is identical with that of the Bay; *Megaxinus floridanus* is the prevailing species, and all the remaining species, though by no means rare as dead shells, are infrequently found living; thus *Arca transversa, Venus campechiensis, Chione cancellata,* etc. Where the mangrove roots touch the open water on the outer edge of the coastal vegetation belt, they are settled by thick colonies of *Ostrea virginica* Gmelin, the so-called tree oyster, and by the mytilid *Brachidontes exustus;* this latter settles only upon the extreme tips of the roots, and therefore never becomes uncovered at low tide, as the tree oysters do; these share their station with the littorinid snail *Littorina angulifera* Lamarck; numerous specimens of the flat oyster pest, *Crepidula plana* Say, are present on and between the crowded shells of the oysters. This marine zone is very narrow, for only a few yards away, within the mangrove belt, sedimentation is rapid. The new bottom within the mangrove zone, still covered by some inches of water at high tide, is thickly overgrown with salt purslane, *Sesuvium portulacastrum,* a plant belonging to the family of the Aizoaceae. It shelters only one bivalve, the corbiculid *Polymesoda floridana* Conrad. This is usually an inhabitant of brackish water, but lives here in ocean water. Two species of gasteropods, the basommatophorous *Melampus coffeus* Linnaeus and the prosobranch *Cerithidea scalariformis* Say, live on and between the salt purslane. Dead valves of *Arca transversa* and *Megaxinus floridanus* scattered over the surface of the alluvial bottom suggest a recent encroachment of vegetation into this area, or may be due to transportation by a storm; in either case, they do

not live in this depositing zone where the three species of mollusks cited above dominate.

Mollusks of Tarpon Bay.—A special biotope on the San Carlos Bay coast of Sanibel Island is presented in Tarpon Bay, an oval basin about one by one and three quarter miles in size, separated from San Carlos Bay by oyster reefs, settled by mangrove. With a single exception, the outlets between the various reefs are too shallow even for motor launches. The shores of Tarpon Bay and their underground condition are almost identical with those of San Carlos Bay in general; the depth nowhere exceeds six feet. On sandy, shallow places, *Megaxinus floridanus* is the most common species; the somewhat deeper spots, where eel grass grows, present a more muddy bottom, with numerous *Venus campechiensis* and *Pinna rigida.* The deepest spots, with a clay bottom, are characterized by the presence of *Chione cancellata.* The fine ridges and ribs on the outer surface of the last-named species and on young *Venus campechiensis* are much more pronounced in Tarpon Bay specimens than in those collected on the Gulf coast. These features seem to be due only to a different degree of wear in the shells; on the Gulf coast, the surf grinds the outer surface of the shells by means of sand particles, often reducing the ribs and ridges to fine traces, while in the almost stagnant water of Tarpon Bay the shells retain their sculpture. A special feature of Tarpon Bay consists of long, narrow oyster reefs that extend almost across the basin; they remain uncovered at low tide and bear only a few young mangrove trees. These apparently recent reefs resemble in all other respects those in San Carlos Bay.

Mollusks of Clam Bayou.—The inevitable filling in of the inlets of the Bay coast has already taken place in a canal, Clam Bayou, opening into the San Carlos Bay in the northeastern part of the Island. Its innermost part, with a white, sandy bottom, exposed at low tide, is settled by mangrove; fiddler crabs (*Uca* sp.) and a purplish red phase of the corbiculid bivalve *Polymesoda floridana* live in this area. The small bivalve apparently was formerly very numerous in the sand flats of Clam Bayou, as is obvious from the many fresh, but empty shells; but its population has been decimated, and even locally annihilated by raccoons, which are common on the island. There are no other living bivalves in this community, but odd valves of the common littoral species are still scattered over the bottom, remnants of the time when these sand flats were still an inlet of San Carlos Bay. The gasteropods *Melampus coffeus, Littorina angulifera,* and *Cerithidea scalariformis,* all on the mangroves, and the last also on the floor below the surface of the water, complete the limited fauna of Clam Bayou.

Mollusks of the Mangrove Flats.—Everywhere on the Bay coast of Sanibel where the mangrove, with the support of the salt purslane, has completed the conquest of the broader inlets, and where these have been filled in, habitat conditions are changed; this is made evident by the shell features of the mollusks inhabiting these flats. The *Polymesoda* living here are grayish, more elongated, triangular, and more convex; no other bivalves are found together with them, their only mollusk companions being *Melampus coffeus* and *Cerithidea scalariformis;* in the dense population of the salt purslane this last-named

species is never as numerous as in the open water and on the mangroves of the sand flats in Clam Bayou. Despite the identical features of like exposure to the air at low tide and similar exposure to the rapacity of raccoons, there are basic differences, due to the consistency of the bottom. There can be no doubt that the soil in the mangrove swamp is essentially denser and more solid than that of the sand flats of Clam Bayou, and this difference is obviously due to the development of the mangrove into tall trees, and to the thick growth of the salt purslane, which causes the soil to appear almost green. These different environmental conditions may be responsible for the different shell shapes and colors of *Polymesoda floridana* in the two habitats, as well as for the comparative rarity of fiddler crabs (*Uca* sp.) in the mangrove swamp.

Mollusks of Blind Pass.—If a creek or bayou opening to the Bay side of Sanibel Island is blocked by a sand-bar at its mouth, the composition of its fauna undergoes marked changes, even if the closure is only at low tide. The modified conditions of life are chiefly due to the almost complete absence of surf, and to the consequent calmness of the water in which the inorganic particles introduced by the flood tide deposit as soft mud. Blind Pass, close to the NW point of Sanibel Island, which formerly opened into San Carlos Bay, is now modified into a lagoon ending blindly at the south, but, as the result of a hurricane in 1926, is connected at the north over a sand bar with the Gulf. The tide in Blind Pass, now entering only from the Gulf, is approximately eighteen inches high and the blind end is exposed at low tide; it has already been settled by mangrove and *Sesuvium,* and changed into an incipient mangrove swamp. If geographical conditions do not change, the whole of Blind Pass will progressively become a mangrove swamp.

The shells on the banks of Blind Pass are witnesses to an original fauna similar to that of the Bay coast of Sanibel Island; but many of the species have disappeared with the change in conditions since 1926. The present fauna of Blind Pass lagoon is impoverished. The rapacious prosobranch snails *Busycon perversum* and *Melongena corona* Gmelin prey on their victims in the shallow water, whereas *Strombus pugilis,* which is so frequent in the still water of the Gulf coast, seems to be absent in Blind Pass. The mytilid *Brachidontes exustus* settles in clusters and in bunches on all objects projecting from the muddy bottom, mostly in company of a barnacle (*Balanus* sp.). Tow species of prosobranchiate snails in very unequal numbers share these areas, often giving a blackish cast to the originally white beach. These are *Cerithium muscarum* Say, found also on the Gulf coast, and the much more numerous potamidid *Batillaria minima* Gmelin. Alert crabs (*Callinectes sapidus* Rathbun) swim in the transparent waters, and the archaic horse-shoe crab *Limulus polyphemus* Linnaeus enters the lagoon every spring to breed. Its young develop to a length of about three inches before they return to the open Gulf. Several species of sedentary polychaetes reside in the mud of the bottom, together with a small marine venerid bivalve, *Anomalocardia cuneimeris* Conrad, which I have not been able to find at all on the Gulf coast or, in a living state, in the sounds that separate Sanibel Island from the mainland. This shell does not occur in the outer open part of Blind Pass, but only in the

blind inner one. It is first seen where the fiddler crabs (*Uca* sp.) begin to appear on the banks of Blind Pass; this bivalve first becomes gradually more numerous and then becomes rarer and rarer and is absent in the extreme inner part of the lagoon. The sand crab or ghost crab, *Ocypode albicans* Bosc, which inhabits the Gulf beach only about 150 yards distant, only rarely visits the banks of Blind Pass.

Toward the blind end of the pass with its mangrove and salt purslane, *Anomalocardia cuneimeris* finds a companion in the corbiculid bivalve *Polymesoda floridana,* mentioned above as an inhabitant of the filled-in shores of the Bay Coast; neither of these situations contains brackish water, which is the general habitat of corbiculid mussels. The color of the shell in specimens from the outer end of Blind Pass is pale greyish yellow, while specimens in the innermost tapering part of the lagoon, where the bottom is bared during low tide, are rich purplish brown with a gradual transition from one color to the other in the intermediate area. *Polymesoda* becomes more and more numerous toward this filled-in part of Blind Pass with its vegetation of mangrove and salt purslane. There *Polymesoda* is the only bivalve to be found, and despite its being exposed to the air for six hours twice a day, the species is so numerous that one grasps ten or fifteen individuals in a single handful of sand. The only mollusk associated with it is *Melampus coffeus.*

Blind Pass, which is intermediate between the Gulf and the Bay coasts of Sanibel Island, has received its fauna from both sides of the island. The presence of true Gulf species, of *Cerithium muscarum* for instance, is due to the connection with the Gulf, while that of *Polymesoda floridana* is explained by the former relation to the Bay coast. *Batillaria minima* and *Anomalocardia cuneimeris* are inhabitants of inland waters of the Floridan west coast in general; their occurrence in Blind Pass is therefore not surprising. My failure to find them alive on the Bay coast of Sanibel may well be accidental. The fauna of Blind Pass is a mixture of true gulf species, of species characteristic of the bays, creeks, and lagoons, and finally of species inhabiting impoverished and often brackish waters and sounds.

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The Occurrence of a Rare Filariid Nematode from a Crow*

B. B. Morgan and E. F. Waller

During the winter of 1939 the writers had the opportunity to examine thirty-six eastern crows *(Corvus brachyrhynchus brachyrhynchus)* which were submitted to the Wildlife Disease Laboratory, Department of Veterinary Pathology, Iowa State College. The crows had been shot for bounty in Des Moines County, near Burlington, Iowa.

The crows were heavily parasitized with various species of lice, nematodes, and cestodes. In one crow several filariid nematodes were recovered from the abdominal cavity. Five female and four male parasites were present which later were identified as *Diplotriaena tricuspis* (Fedtsch, 1874).

Family: FILARIIDAE (Cobbold, 1864)
Subfamily: DIPLOTRIAENINAE (Skrjabin, 1916)
Genus: DIPLOTRIAENA (Railliet and Henry, 1909)

The genus Diplotriaena was established to include a particular group of very closely related species of Filaria which were found in the body cavities of various birds, mainly in Strigiformes and Passeriformes.

This genus can be readily recognized by the presence of a structure in the form of a pair of chitinous trident-like processes. These tridents are located at the anterior extremity. Another characteristic of this genus is the structure of the male spicules, one of which is straight, the other twisted spirally for approximately one or two turns.

Approximately thirty species have been placed in this genus. The majority of the original diagnoses has been so poorly and inadequately described that the species identification is very difficult. Schmerling (1925) published a key to the species which is now obsolete because numerous species have been named since the appearance of his article.

Diplotriaena tricuspis (Fedtsch, 1874)

Description.—Body long, slender, and cylindrical; attenuated at the extremities, more so at the anterior than at the posterior portion. The mouth is simple, oval in shape, small, and no lips present. There are four pairs of submedian cephalic papillae, all about equal in size. The cuticle is not transversely striated. The chitinous tridents are very conspicuous located one on

* A joint contribution from the University of Wisconsin, Departments of Zoology and Veterinary Science and Iowa State College, Department of Veterinary Pathology, Project 570 in cooperation with the U. S. Biological Survey, the American Wildlife Institute, and the Iowa Conservation Commission.

each lateral side of the anterior end of the esophagus. They range in size from 120-180 microns. The esophagus is divided into two portions, short narrow muscular anterior portion 260 microns long, and a long rather broad glandular posterior portion 4.5 mm. long. The nerve ring surrounds the center of the anterior portion of the esophagus. The excretory pore is just posterior to the mouth and rather prominent. The intestine is heavily pigmented.

Male 50 to 55 mm. long and approximately 750 microns wide. The tail is very short, only 125 microns long, and bluntly rounded. There are four pairs of pre-anal and two pairs of post-anal papillae which are simple and arranged irregularly. The spicules are very unequal in length and dissimilar in shape: the left spicule being straight and 1.4-1.5 mm. long, the right spicule twisted spirally and approximately 800-900 microns long.

Female quite large reaching a length of 104-190 mm. and measuring 1.2 mm. in maximum width. The anal pore is subterminal. The vulva is approximately 430 microns from the anterior end. The stout muscular vagina or ovijector runs straight backwards and is approximately 4-5 mm. long and divides into two uteri. The uteri are found in numerous coils around the intestinal tract. The female is oviparous, the eggs having thick shells and measuring 35 x 45 microns. The embryos are distinct and well developed.

Host.—Eastern Crow *(Corvus brachyrhynchos brachyrhynchos). Habitat.*—Body Cavity. *Locality.*—Burlington, Des Moines County, Iowa.

Discussion

Leidy (1886) first found this parasite from the body cavity of a boat-tailed grackle *(Megaquiscalus major)* from Florida which at the time was identified as a new species, *Filaria cirrura.* Walton (1927) in a redescription of this parasite found it to be *D. tricuspis* and not *F. cirrura.* This marked for the first time the occurrence of this parasite in the United States as the former distribution was entirely Old World in extent. Walton (1927) also recorded *D. tricuspis* from the chewink or towhee *(Pipilo erythropthalmus)* from the Leidy collection. The bird was obtained from Florida. So far as the writers are aware these are the only records of *D. tricuspis* in American hosts. Boughton (1938) reported the microfilaria of the eastern crow in Georgia but does not mention the finding of the adult nematode. One of us (B.B.M.) has found this parasite in a crow from Wisconsin *(Corvus brachyrhynchos brachyrhynchos).* Other microfilaria recorded from North American birds are: Baltimore oriole *(Icterus glabula),* orchard oriole *(Icterus spurius),* red-breasted grosbeak *(Hedymeles ludovicianus),* yellow-billed cuckoo *(Coccyzus americanus),* black-billed cuckoo *(Coccyzus erythropthalmus),* mourning dove *(Zenaidura carolinensis),* and the magpie *(Pica hudsonia).* The various hosts were obtained from Nebraska by Coatney and Roudabush (1937).

Boulenger (1920) reported *D. tricuspis* from the white-headed starling *(Poliospar leucocephalus)* in England. Monnig (1923) recorded this parasite from South Africa in an owl *(Otis ruficresta).* Yorke and Maplestone (1926)

listed the original hosts in which this parasite was described from a crow *(Corvus cornix),* and *Alaemon duponti.* Later Boulenger (1928) added two more crows *(Corvus cornix* and *C. umbrinus)* to the host list of this parasite. These birds were from Egypt. Canavan (1929) reported *D. tricuspis* from the pileated jay *(Cyanocorax chrysops)* obtained from Brazil and Uruguay. Later Canavan (1931) recorded three more hosts for *D. tricuspis:* Indian mynah bird *(Acridotheres ginginianus)* from North India, Columbian jay *(Cyanocorax affinis)* from Panama and Colombia, and the black-winged mynah bird *(Graculpica melanoptera)* from Java. In (1933) Li recorded four more crows to the host list of *D. tricuspis* from North China. The hosts are as follows: *Corvus sinensis, C. neglectus, C. corax,* and *C. torquatus.*

Summary

First occurrence of *Diplotriaena tricuspis* in Iowa with a newly recorded host, the eastern crow *(Corvus brachyrhynchos brachrhynchos).* A brief description of the parasite is included.

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New Species of Corals from the Bainbridge Limestone of Southeastern Missouri

John R. Ball and Brandon H. Grove

The Bainbridge limestone is a formation of late Niagaran age cropping out in several places in the area of faulted Paleozoic rocks in Ste. Genevieve county and also farther south in Missouri, along the Mississippi River.[1] The type section is about three miles north of Bainbridge, in Cape Girardeau county, Missouri. Some of its fossils were described by Rowley in 1900 and 1904.[2] Tentative faunal lists were published in 1926[3] and 1928,[4] the one of later date having been prepared by Stuart Weller much earlier than the list presented in 1926, and published without revision. A more comprehensive faunal list was published in 1927[5] and a description of a few of the brachiopods appeared in 1931.[6] A brief faunal list of the type section of the Bainbridge limestone was read at the Toronto meeting of the Paleontological Society,[7] and an abstract of a paper read at the Houston meeting of the American Association of Petroleum Geologists has been published.[8]

More recently a detailed description of the type section of the Bainbridge formation has appeared[9] with a partial list of the fossils appearing in that section. Some of the characteristic fossils of the Bainbridge formation are mentioned in the Guidebook[10] of the 1939 Annual Field Conference of the

1 Weller, S., and St. Clair, S., 1928—Geology of Ste. Genevieve County, Missouri. Missouri Bur. Geol. and Mines, **22**: (second series).

2 Rowley, W. W., 1900—New species of Crinoids, Blastoids and Cystoids from Missouri. Amer. Geol. **25**:65-75. *Id.*, 1904—The Echinodermata of the Missouri Silurian and a new brachiopod. Amer. Geol. **34**:269-283.

3 Flint, R. F., and Ball, J. R., 1926—Revision of the Silurian of southeastern Missouri. Jour. Geol. **34**:248-256.

4 Weller and St. Clair, *op. cit.*, 130.

5 Ball, J. R., 1927—The faunas of the Brassfield and Bainbridge limestones of southeastern Missouri. University of Chicago Abstracts of Theses, Science Series, **5**:261-269.

6 Ball, J. R., and Dunn, P. H., 1931—Some new species of *Camarotoechia* from the Bainbridge limestone of Missouri. Trans. Ill. Acad. Sci. **24**:380-391.

7 Ball, J. R., 1931—Faunal list from the type section of the Bainbridge limestone of Missouri. Bull. G. S. A. **42**:352. (Abstract).

8 Ball, J. R., 1933—*Bainbridgia typicalis;* new genus and species of Silurian Auloporidae. Pan-Amer. Geol. **59**:239-240. (Abstract).

9 Ball, J. R., 1939—Type section of Bainbridge formation of southeastern Missouri. Bull. Amer. Assoc. Pet. Geol. **23**:595-601, 3 figs.

10 Ball, J. R., 1939—Stratigraphy of the Silurian System of the Lower Mississippi Valley. Guidebook, 13th Annual Field Conference, Kansas Geol. Soc., **13**:110-126, 3 figs.

Kansas Geological Society. Ball and Delo[11] have described the new species of *Dalmanites* which have been secured from the Bainbridge formation in Ste. Genevieve and Cape Girardeau Counties, Missouri.

In the present paper the senior author has revised his earlier studies of *Striatopora, Cladochonus* (?) and *Bainbridgia*. He is responsible, also, for the original selection of the specific names used for the new species. The junior author has described the morpology and ontogeny of the Tetracoralla and has revised the original descriptions and illustrations of those forms. He has attended to the photography and has made the thin-sections and camera-lucida drawings used in the text figures and plates.

ACKNOWLEDGMENTS

The study of the Bainbridge corals was inaugurated under the direction of the late Stuart Weller, who furnished inspiration for the work and gave faithful attention to the initial development of the task. The authors are indebted to Dr. Carey Croneis for the use of facilities in Walker Museum and for his sustained interest in the study. Dr. Croneis has read the manuscript in part and has made many stimulating suggestions. Dr. R. S. Bassler has loaned specimens of Auloporidae from the Smithsonian Institution, has read the description of *Bainbridgia typicalis* and has offered helpful comments. Dr. R. M. Ehlers has loaned the types of *Romingeria* from the Paleontological Museum of the University of Michigan and has given appreciated advice in conference and by correspondence. Dr. R. C. Moore has made thin-sections of *Bainbridgia* and has aided the authors in their judgment concerning the affinities of this coral.

Dr. Winifred Goldring has answered many questions for the writers most cordially, has secured enlarged prints of *Laccophyllum acuminatum* for them, and has compared specimens of *L. petaloides* sp. nov. with the genoholotype at Albany. She has also kindly kept the writers informed of the opinions of European students of corals concerning the possible congeneric relations of *Laccophyllum* with several other Silurian and Carboniferous genera.

Analysis of the Bainbridge Corals

The corals constitute about one-tenth of the known Bainbridge macrofauna. In the following table the new species are separated from those previously known:

Described species	New species
Laccophyllum acuminatum Simpson	*Laccophyllum petaloides*
Enterolasma waynense (Safford)	*Diteoecholasma saffordi*
Favosites discoideus (Roemer)	*Striatopora spiralis*
Favosites cf. *obpyriformis* Foerste	*Cladochonus* ? *siluriensis*
F. forbesi occidentalis Hall	*Bainbridgia typicalis*
Striatopora flexuosa Hall	*Bordenia savagei*

Of the known species, the first four are believed to have been reported previously only from the Brownsport beds of Tennessee. *Favosites forbesi occidentalis* occurs in the Waldron beds of Indiana, and *Striatopora flexuosa* is more widely distributed in North America.[12]

11 Ball, J. R., and Delo, D. M., 1940—New species of Silurian Dalmanites from southeast Missouri. Amer. Mid. Nat. **24**(2):405-410.

12 Bassler, R. S., 1915—Bibliographic Index of American Ordovician and Silurian fossils. U. S. Nat. Mus. Bull. **92**, vols. 1, 2.

Ross Maxwell and the senior author have shown that the species *Laccophyllum acuminatum, Enterolasma waynense* and *Striatopora flexuosa* occur in the Henryhouse formation of the Arbuckle Mountains, and that *Laccophyllum petaloides* sp. nov. also occurs in that formation.[13] Species in addition to those listed above probably occur in the Bainbridge and Henryhouse formations, particularly among the Tetracorals, most of which are externally very similar and commonly have their calyxes so concealed with a filling of matrix that they must be ground for identification.

The coral fauna of the Bainbridge is strikingly parallel to that described by Pocta[14] from the Silurian basin of Bohemia, except for the much smaller number of forms thus far identified in the Bainbridge. Our Laccophyllidae appear closely related to the *Syringaxon (Nicholsonia)* and *Barrandeophyllum* of Bohemia, and a number of the Auloporidae described by Barrande and Pocta appear only specifically different from the *Bainbridgia* and *Cladochonus* ? of the Bainbridge. Even the rather unusual *Bordenia* of the Missouri Silurian seems to have a distant relative in the *Microplasma* of Bohemia. On the other hand something of this resemblance is fairly to be expected inasmuch as Butler,[15] Prantl,[16] and others are pointing out the probabilities of congeneric origin among many of these forms.

Stratigraphic Distribution of the Corals

The corals are well distributed vertically through the Bainbridge formation in Ste Genevieve county, and in two horizons they are fairly common. One is near the base of the formation in a shaly facies which furnished the specimens described by Rowley. Although apparently a restricted lentil, it has been called for convenience the *Pisocrinus* zone[17] and notwithstanding frequent visits from collectors still yields many echinoderms, corals, bryozoa and brachiopods.

The other coral horizon is at or near the top of the Bainbridge formation. Here, both in Ste. Genevieve and Cape Girardeau counties, the *Bordenia, Bainbridgia* and *Striatopora* occur abundantly. In Cape Girardeau county these fossils are in a hard, thin-bedded, purple and reddish limestone; in Ste. Genevieve county they are in the weathered fragments of a gray, argillaceous limestone.

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13 Ball, J. R., and Maxwell, R. A., 1935—Correlation notes on the Bainbridge formation of Missouri and the Henryhouse formation of Oklahoma. Proc Geol. Soc. Amer. 391. (Abstract).

14 Pocta, P., 1894—In Barrande, J., Systéme Silurien du centre de la Bohême **8**: pt. 1. Id. pt. 2, 1903.

15 Butler, A. J., 1935—On the Silurian coral *Cyathaxonia siluriensis* M'Coy. Geol. Mag. **72**:118.

16 Prantl, Ferd., 1938—Some Lacophyllidae from the Middle Devonian of Bohemia. Ann. Mag. Nat. Hist., 11th ser., **2**:21.

17 Ball, J. R., 1927—The faunas of the Brassfield and Bainbridge limestones of southeastern Missouri. Univ. of Chicago Abstracts of Theses, Science Series **5**:265.

Description of Species

Subclass TETRACORALLA Haeckel

Family LACCOPHYLLIDAE Grabau

Genus *Laccophyllum* Simpson

Laccophyllum Simpson, Bull. N. Y. State Museum, 39, 1900: 201-202, figs. 7-9.

Laccophyllum petaloides sp. nov.

Plate 2, Figs. 3-6; Pl. 4, figs. 1-5, 7-10

Description.—Corallum simple, small, subconical, expanding rapidly from the base, slightly curved. Calyx relatively deep, calyx floor in many specimens flush with the top of the corallum due to breakage of the thecal wall. Septa radially arranged, delicate, sub-equal in size, primaries and secondaries indistinguishable in the calyx. No fossula. For two-thirds or more of their length the septa extend towards the axis in pairs, thereafter each pair fuses into a single septum, the distal end of which bends slightly and coalesces with its neighbors to form a phyllotheca which bounds a central tube-like opening characteristic of *Laccophyllum*. The tube thus formed occupies the central quarter of the diameter of the calyx, and its top is deeply excavated. In mature specimens the septa are arranged in from sixteen to twenty-one pairs, each pair forming an elongated triangle with apex toward the center, giving a petaloid aspect to the calyx. In some instances the septa resemble delicate tubes with surfaces nearly smooth lying upon a diaphragm.

The exterior of the corallum bears rounded rugae regularly arranged, with slight annular ridges and striations appearing in abundance on some specimens. The dimensions of one of the larger specimens are: Length, 15.4 mm.; greatest diameter of calyx, 9.7 mm. Of a specimen nearer the average size the length is 9.5 mm.; greatest width of calyx, 6 mm.

Internal characters.—The earlier ontogeny of *Laccophyllum petaloides* is illustrated schematically in Fig. 1, which indicates the mode of septal insertion from the close of the brephic to the commencement of the ephebic stages. Despite the grinding of a considerable number of specimens, we have been unable to find tips which preserved the relative developments during the brephic stage, as sections cut within a millimeter from the end of apparently well preserved tips already showed ten to twelve septa. The earliest stage shown in Fig. 1 is noteworthy in that it shows a secondary septum of the counter quadrants which in each case is as well developed as the corresponding alar septum, and apparently plays a similar role. Thus at the close of the brephic stage there are eight septa of primary value present. With regard to the second stage schematized in Fig. 1, we were not able to determine the relative sequence in which the new septa appeared, but could only confirm that two new secondary septa were developed in each quadrant during the phase covered by this sketch. The insertion of new septa during the neanic period is indicated by the remaining sketches of Fig. 1, and is show by camera lucida drawings from a single specimen in Figs. 1-4 of plate 4. Noteworthy in the late neanic stage is the pairing of the cardinal septum; in this connection it may be noted that

the counter and counter-lateral septa do not become correspondingly paired until late in the ephebic stage (see Fig. 2). Figs. 7-10 of Plate 4 are camera lucida drawings from a single specimen and show the aspects of the septa during the later ephebic and gerontic stages.

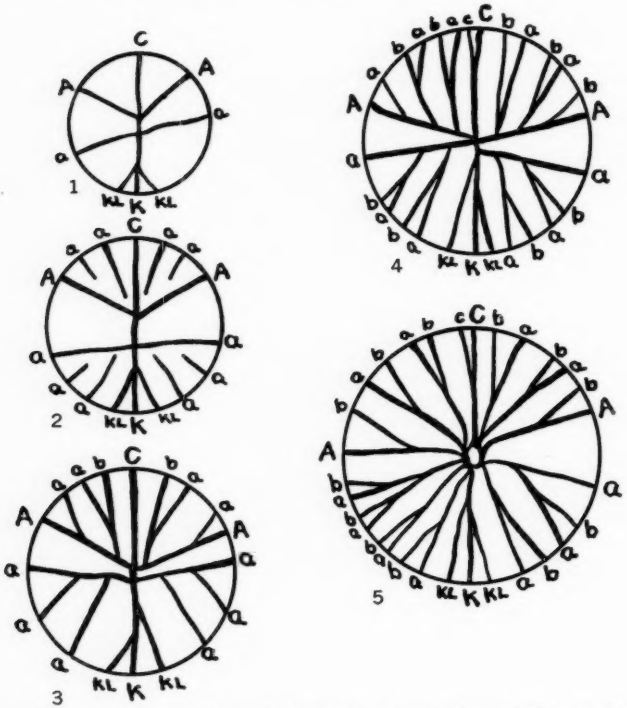

Fig. 1. Diagram to illustrate the mode of septal insertion in *Laccophyllum petaloides*.

There is no development of tertiary septa in *Laccophyllum petaloides*, and in a mature calyx all septal pairs appear to be of equal value, giving a truly radial symmetry. During development, new septa are inserted immediately adjacent to the older ones; to all appearances, indeed, budding directly from them, and during the course of growth thereafter migrate toward the axis and along the circumference in the direction of the cardinal septum. Except for the information gained from the study of the early ontogeny, it would commonly be impossible to tell which septum of a well-developed pair was the older.

The diaphragm-like appearance of the calicular floor noted in the description of the external characters has resulted from the nearly uniform upbuild-

ing of the space between the two septa of each pair through the deposition of stereoplasm; the alleys between the pairs commonly remain free from such deposits. At no time is there any noteworthy dilatation of the inner portions of the septa in consequence of stereoplasmic deposition.

The longitudinal section shown in Fig. 5 of Plate 4 indicates the development of tabulae and dissepiments, and sheds important light on the structure of the aulos. In general, dissepiments are only very sparsely present, whereas tabulae are moderately frequent and fairly uniformly spaced throughout the corallum. Both tabulae and dissepiments are confined to the space between the theca and the inner wall. The structure of the aulos is of particular interest: Its basic framework results from the twisting and fusion of the inner ends of the septa. Within the tube thus formed a deposit of stereoplasm is laid down which partitions it completely and then grows upward as a lining. At intervals which increase in rough proportion to the increasing size of the corallum, similar new stereoplasmic partitions are formed, which in their turn continue

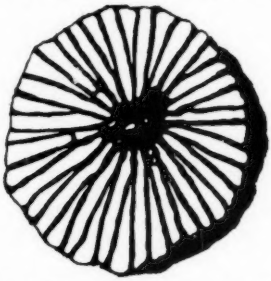

Fig. 2. *Laccophyllum petaloides;* camera ludica drawing showing septal arrangement in mature forms.

upward as a lining for the aulos, the older deposits enveloping the new ones for short distances and then merging indistinguishably with them. The resulting structure resembles a series of thimbles inserted one within the other to produce a tube, the end of each such "thimble" appearing in longitudinal section like a heavy tabulum within the aulos.

Septal acceleration in *Laccophyllum petaloides* is most apparent during the neanic stage, during which development takes place most rapidly in the counter quadrants. Fig. 2 of Plate 4 illustrates a section cut at an angle so as to include a higher section in the cardinal as compared with the counter quadrants, and andicates the more rapid septal insertion in the latter.

In the course of sectioning a considerable number of specimens of *L. petaloides* we have observed that some of them exhibit a phenomenon of retardation. Such forms are in all external characters identical with normal specimens, but in them the septal arrangement characteristic of the neanic stage in most individuals of the species is retained until late in what is the ephebic stage so far as concerns the size of the corallum and the number of

septa present. Before attaining full maturity, however, these forms develop an aulos and become identical with the others. Fig. 5 of Plate 4 appears to have been cut from such an individual, and it may be observed in it that the aulos occupies only the upper half of the corallum, whereas in the majority of specimens it runs nearly the entire length of the corallum. This peculiarity might form justifiable basis for the erection of a variety if there were any means of detecting it short of grinding away a good part of the specimen. We have found a single specimen in which this condition appears to have persisted into maturity, and further search may ultimately indicate that a new species has arisen in this manner.

Remarks.—*Laccophyllum petaloides* is closely related to *L. acuminatum* Simpson, from which it may be distinguished by the greater number of septa, their more markedly paired arrangement, the nearly equal size of both septa in most pairs, and the fact that dissepiments are much less frequent than in *L. acuminatum*. In *L. petaloides* the cardinal, counter and counter-lateral septa become components of a pair in full maturity, whereas in all specimens of *L. acuminatum* observed, these septa have remained single. External differences, not invariably reliable, are to be found in the oval cross-section of the calyx in *L. acuminatum* as compared with the nearly round one of *L. petaloides*, and in the somewhat larger average size of the former species. In the course of our study we have made tip sections from specimens of *L. acuminatum* from the Bainbridge; these seem to indicate that septal insertion is essentially identical during the earlier stages of both species.

In assigning our species to the genus *Laccophyllum* Simpson we have given careful consideration to the possibility that this genus may be so closely related to *Syringaxon* M'Coy as ultimately to be considered congeneric. The stages of septal insertion diagrammed in Fig. 1 agree very well with those determined by Butler[18] for *Syringaxon*, stage 1 of our figure corresponding with Butler's Fig. 3, and stage 3 with his Fig. 9. *Syringaxon (Nicholsonia) Bohemica* Barrande and *Barrandeophyllum perplexum* Pocta likewise appear related to *Laccophyllum petaloides* and *L. acuminatum*, a resemblance which is particularly true of the neanic section of *B. perplexum* figured by Pocta.[19] On the other hand, the description of the formation of the aulos in *L. petaloides* given above indicates that the genus Laccophyllum differs from *Syringaxon* and *Barrandeophyllum* as much as these genera differ from one another, and must be considered valid at least until the criteria for Tetracoral genera are broader and better standardized.

Occurrence.—*Pisocrinus* beds of the Bainbridge formation, red and purple shales, St. Mary's road, about 2¼ miles southeast of Ozora, Ste. Genevieve county, Missouri.

Types.—Holotype, No. 34511, Walker Museum, The University of Chicago (Figs. 4-5 of Pl. 2). Paratypes, No. 45188 and No. 45187, Walker Museum (Figs. 3 and 6 of Pl. 2). The specimen of Fig. 6 has been sectioned

18 Butler, A. J., *op. cit.*, p. 120, figs. 1-9.

19 Pocta, P., *op. cit.*, pl. 108, fig. 4.

to give Fig. 2 on page 387; the specimen of Fig. 3 is an entire corallum with the upper end of the phyllotheca well exposed by weathering. Thin-sections No. 39151, Walker Museum.

Genus *Ditoecholasma* Simpson

Ditoecholasma Simpson, Bull. N. Y. State Museum, 39, 1900: 200-201, figs. 5-6.

Ditoecholasma saffordi sp. nov.

Plate 2, Figs. 7-10; Pl. 4, Fig. 6

Description.—Corallum simple, small, subcylindrical, straight or slightly twisted especially near the tip, very gradually increasing in size. Rugae distinct, and attachment scar frequently visible. Calyx moderately deep, and in mature specimens containing twelve to fifteen pairs of septa in addition to four unpaired primaries (the cardinal, counter and two counter-laterals). The septa of each pair join near the center of the calyx, and are continued to the axis as a single blade. Each septal pair is separated from the adjacent pairs by a relatively narrower interspace. Tertiary septa not observed and probably non-existent.

Average dimensions of mature coralla: Length, 13 mm.; diameter of calyx, 5 mm.

Internal characters.—We have been unable to find material in which the neanic and brephic stages were visibly preserved, and our description of the internal structure is necessarily confined to the ephebic portions of the corallum. At this stage the pattern shown by the septa in transverse sections is essentially that of the calyx (Fig. 6, Pl. 4). The septa show a distinct grouping, not merely into pairs, but into units composed of two pairs. The point of union for the component pairs of such groups varies from about a third of the distance to the axis to nearly at the axis itself. After their fusion, the septa of each group are continued to the center as a single blade, which at the center of the corallum fuses with other such blades to form a streptocolumella. In the later ephebic stages (Pl. 2, Fig. 7) the septal grouping becomes obscured. The cardinal, counter, and counter-lateral septa remain distinct and unpaired throughout the mature portions of the corallum. Dissepiments appear to be absent.

The diagnostic characters of the species are only visible in longitudinal sections (Pl. 2, Fig. 10). Such sections show the streptocolumella occupying the central quarter, or slightly more, of the corallum, and extending nearly its entire length. It is of very chain-like aspect, and appears to have resulted from the fusion of the irregularly waved inner edges of the septa, and to have been reinforced with a light deposition of stereoplasm. The space between the columella and the theca is partitioned by regularly spaced, nearly horizontal tabulae. More striking than these latter, however, is the partitioning of the entire corallum into three or four sections, which is effected by what appear to be very heavy tabulae which start at the columella and extend upwards at an angle of about 45 degrees to join the theca.

Remarks.—Simpson based his description of the genus *Ditoecholasma* on *Petraia fanningana* Safford, a form which occurs in the Brownsport beds of Perry county, Tennessee. Unfortunately, Safford's description of his species is restricted to a citation in a faunal list and a series of very undiagnostic sketches in one of his plates.[20] However, the resemblance between Safford's sketches and the external appearance of our species is so great that no tangible basis exists for their separation on this ground. We have therefore relied on the internal characters illustrated by Simpson in erecting the genus *Ditoecholasma,* in concluding that the Bainbridge forms constituted a separate species. Safford states that he customarily sent samples of his material to Hall, and it seems reasonably probable that Simpson's sections were cut from specimens collected by Safford at the type locality. On this basis there can be no question of specific identity, for Simpson's figure[21] shows a form containing dissepiments rather than tabulae, and lacking the large partitioning tabulae described above.

It is to the Silurian of Bohemia that we must look for the nearest described relative of *Ditoecholasma saffordi.* The sketch of *Streptelasma Bohemica* figured by Pocta[22] shows a form which is not only a *Ditoecholasma,* but could conceivably be conspecific with the Bainbridge species if its characters were available for detailed comparison.

Occurrence.—*Pisocrinus* zone of the Bainbridge formation, Ste. Genevieve county, Missouri.

Types.—Holotype, No. 39352, Walker Museum, The University of Chicago (Figs. 8-9 of Plate 2). Thin sections, Nos. 39356 and 39360, Walker Museum (Figs. 7 and 10 of Plate 2).

Family Zaphrentidae Milne-Edwards and Haime
Genus *Bordenia* Greene

Bordenia Greene, G. K., Contr. to Ind. Pal., Vol. 1, pt. 7:57, pl. 19, figs. 2-9, 1901.
Bordenia zaphrentiformis Greene, Beede, J. W., 30th Ann. Rept., Ind. Dept. Geol. and Nat. Res., 1205-6, pl. 7, figs. 6-6c, 1905.

Original description.—"Corallum simple or composite, resembling Zaphrentis. Tabulae complete with the central portion being smooth. Fossette well pronounced or scarcely more than rudimentary. Primary lamellae well defined. Secondary lamellae rudimentary or indicated by fine striae. Type *B. zaphrentiformis.*"

From the characters of the type species, and from the exposition of *Bordenia* subsequently given by Beede, it is apparent that Greene considered reproduction by fission to be the fundamental character diagnostic of this genus. Both the type species and those described later by Greene and Beede show a tendency to retain the products of fission so that coralla composed of two, three or more corallites are common.

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20 Safford, J. M., 1869—Geology of Tennessee. P. 320, pl. H, figs. 3a-3g.
21 Simpson, G. B., *op. cit.*, p. 201, fig. 6.
22 Pocta, P., *op. cit.*, p. 156, fig. 3.

Reproductive habit has been repeatedly shown to be a very untrustworthy character for the differentiation of genera, or even, species. Reproduction by fission is of such rare occurrence among members of the Zaphrentidae, however, that its appearance, coupled with the common formation of composite specimens, seems indicative of the close relationship of the forms exhibiting it and suggests a justifiable basis for their systematic segregation.

Bordenia savagei sp. nov.
Plate 1, Figs 1-8; Plate 2, Figs. 1-2

Description.—Corallum simple or composite, of medium size, slightly curved, and in some cases greatly contorted. Branching or composite forms resulting from reproduction by budding and fission but without complete parting are common. These include many specimens in which both individuals of the composite type are fully mature and, apparently, complete separation would never have occurred. Solitary corallites are numerous, and in these the calyx is shallow, subcircular or elliptical, wall thin, septa of unequal length, commonly twenty or twenty one in number, the longest not extending to the center but commonly blending at the distal ends in a mass of vesicular tissue. In some specimens slightly curving secondary septa are regularly introduced but in others these seem to be lacking. Occasionally a mature calyx may be found containing one or more buds contiguous to the calicular wall. In unweathered specimens annular ridges and striations are distinct, but where weathering is much advanced the rugae are conspicuous.

The dimensions of one of the more elongate speecimens are: Length, 32 mm.; diameter of the calyx at the rim, 10.7 mm.; in an individual expanding more rapidly from the base the dimensions are: Length, 23 mm., greatest diameter of the calyx, 13.2 mm.

Internal characters.—In the mature portions of the corallum the structure of *B. savagei* is essentially that of a coral in the amplexid stage of development, as is illustrated by text-figure 3. The septa are somewhat retracted marginally and there are peripheral dissepiments, limited in number, but zonally arranged. The heavy and complete development of tabulae further evidences an amplexid habit. The development of the tabulae is particularly evident in specimens which have been crushed or are extensively weathered (Pl. 1, Figs. 3, 7).

The longitudinal section illustrated in Fig. 2 of Pl. 2 shows two mature corallites still joined together for perhaps one-third of their diameters, but completely separated for the remaining two-thirds. The section has been cut through two buds in the upper corallite, although only the lower portion of the one to the left is preserved. It can also be noted that in some transverse zones the development of dissepiments is subcystose.

In the neanic portions of a corallum the septal structure is zaphrentid in character. The septa are long, approaching the center of the corallum, and the development of tabulae and dissepiments is much reduced. Whatever the phylogenetic implications of this may be, it appears to have resulted directly from the manner of reproduction by budding. New buds originate in the

calyx, adjacent to the theca. At the point where a new bud is formed, certain septa of the parent corallite undergo a sort of rejuvenation, and grow rapidly upward to form the septal apparatus of the offspring. A new theca forms around them, and commences to resorb the septal connection between the bud and the parent. This resorption may become complete, in which case partition

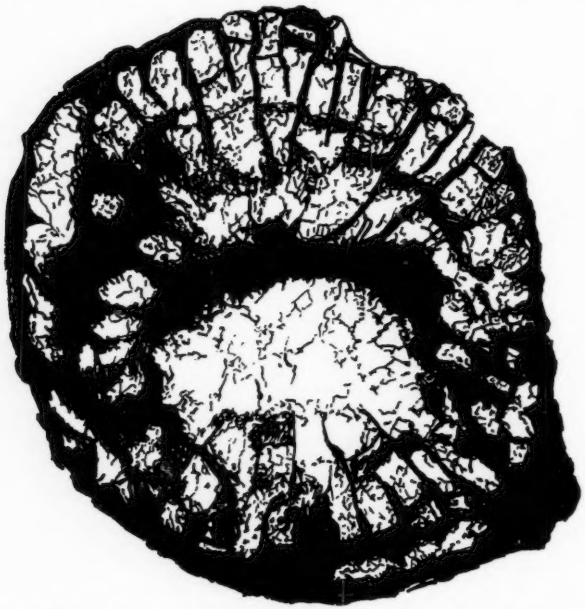

Fig. 3. Transverse section of *Bordenia savagei* in mature portion of corallum.

takes place, or only partial, giving rise to compound forms. After a bud has attained a length of three or four millimeters its septa begin to retract, tabulae and dissepiments undergo marked development, and the amplexid aspect of the mature corallum is achieved.

Remarks.—In earlier studies the senior author had listed this species as one of the genus *Zaphrentis*. From the frequent occurrence of composite coralla in the Bainbridge collections, it seems justifiable to recognize the tendency towards fission reproduction stressed by Greene and to reassign the species to *Bordenia*. In the equally large number of individual coralla the Zaphrentid and Amplexid characters are noteworthy. The species is marked by variability in the outlines of the specimens, some of the contorted cylindrical individuals resembling *Amplexus*. In external appearance and in the arrangement of the septa, as well as in the development of the tabulae, the species

is also strongly suggestive of *Zaphrentis ambigua* Savage. The septa are undulatory, fasciculate, and contrastive in growth, as in that species. The number of primary septa in this species, however, is about half that in *Z. ambigua*, the calyx is shallow instead of deep, and the average size of the specimens apparently is less.

A very close relative of the genus *Bordenia* as typified by *B. savagei* is the genus *Microplasma* Dybowski as illustrated by the species from the Silurian of Bohemia described by Pocta.[23] These forms likewise give rise to composite coralla, but the character of their septal apparatus is predominantly cystose.

Occurrence.—Near the top of the Bainbridge limestone, southwest of the University of Chicago Field Station, about two miles southwest of Ozora, Ste. Genevieve county, Missouri.

Types.—Holotype, No. 34516, Walker Museum, University of Chicago. Paratypes, No. 2293, Paleontological Museum, Northwestern University; No. 45189, Walker Museum.

Subclass TABULATA Milne-Edwards and Haime

Family FAVOSITIDAE Milne-Edwards and Haime

Genus *Striatopora* Hall

Striatopora Hall, James, Amer. Jour. Sci., Arts, 2nd Ser., 400, 1851.

Striatopora spiralis sp. nov.

Plate 3, Figs. 1-4, 12

Description.—Corallum free or encrusting, slender, cylindrical, occasionally branching, the corallites thick-walled, widely separated, distributed in rudely spiral arrangement in the free coralla, the order of their arrangement occasionally broken by the clusters of buds which develop, especially noticeable in the encrusting forms. Corallite apertures nearly circular, gradually expanding, extending from the axis of the corallum in angles of less than 45 degrees and opening into circular or sub-elliptical calyxes. Calyx rims flush with the axial column of the corallum above the apertures and strongly protuberant below, the depressions of the calyxes marked by two elevated, parallel ridges or rudimentary septa which extend upward from the apertures nearly to the rims of the calyxes. Wall of corallum pierced by large pores (budding orifices?) which are distributed with no systematic arrangement. Habit of attachment not observed but the encrusting forms commonly entwine crinoid stems.

Diameters of coralla of about average size 2.8 mm.; diameter of one of the largest specimens 4 mm.; of one of the smallest 1.6 mm. In individuals of average size the longitudinal distance from the center of one aperture to the next is about the same as the diameter of the corallum.

Remarks.—This coral has been collected from weathered rock at or near the top of the Bainbridge formation near Camp Wrather. It is associated with

23 Pocta, P., *op. cit.*, pp. 175-176, pl. 103, figs. 1, 2; pl. 104, figs. 1-4, 8.

S. flexuosa Hall, and, in general outline of coralla and in the occurrence of septal ridges in the calyxes it apparently is a species of *Striatopora*. It differs markedly from *S. flexuosa* in the few and widely separated apertures, in the more circular calyxes, in the spiral arrangement of the corallites and in the more delicate coralla. It differs from *S. huronensis* Rominger in the funnel-shaped calyxes and in the wide separation of corallites.

In free coralla of linear growth the spiral arrangement of the corallites is rarely disturbed by the budding processes and the regularity of spiral and serial arrangement of corallites is consistent in nearly all of the specimens. It seems probable that reproduction took place near the distal end of the corallum.

Slight variations in calyx walls sometimes are apparent, the parallel ridges are absent in some individuals and in others a transverse ridge above the aperture has been observed. In some specimens which entwine crinoid stems, regular arrangement of the corallites is lacking (Plate 3, Figs. 1, 3) and the mural pores are more numerous than in individuals of linear habit.

Occurrence.—In coll about one-quarter of a mile southwest of Camp Wrather, east of private road leading south from the Palmer farm, Ste. Genevieve County, Missouri.

Types.—Holotype, Walker Museum, University of Chicago, No. 45190: Paratype, No. 34520, Walker Museum, (Plate 3, Figs. 4 and 2, respectively).

Family AULOPORIDAE Nicholson

Genus **Bainbridgia** gen. nov.

Description.—Coralla compound, delicate, non-parasitic, flattened cylindrical, increase by lateral gemmation, the corallites issuing in regular alternate succession from the opposite walls of the coralla and maintaining uniform spacing along the stalk. In some specimens a slightly undulating median line is impressed along the corallum (Pl. 2, Fig. 11). In other specimens the line is somewhat discontinuous and in many specimens it is lacking. Direction of growth in the deeply embedded corallites is so nearly parallel with this line that it is suggestive of the projection of a plane of fusion between two tracts of corallites.

Internal character.—Sectional longitudinal views (Pl. 3, Figs. 5-7) show the coralla to be composed of two or more opposed rows of corallites, each row developed in a common coenenchymal tract, the sub-parallel corallites separated by a coenenchymal deposit in which the median plane appears. The corallites occasionally are connected apparently by an opening at right angles to their axes. (Shown possibly above the center of Fig. 5, Pl. 3). In other places, short, transverse extensions proceed from some of the corallites, representing possibly abortive attempts to establish connections. These openings, if to be regarded as such, are not common.

In other respects the coenenchyma, externally and internally, is comparatively featureless. Externally, in some specimens a suggestion of perisarcal

structure has been observed.[24] Tabulae have not been observed but faint lines or ridges suggestive of rudimentary septa are present in a few instances.

Genoholotype: *Bainbridgia typicalis* gen. and sp. nov.

Remarks.—On the assumption that these specimens are actually corals, this genus shows close similarity if not actual congeneric relations with several of the forms reported as *Aulopora* by Barrande and Pocta.[25] Part of the development of the median impressed line is apparent in several of the species described by these authors. The earliest indication of this distinctive marking appears in *Aulopora serrulata* Pocta (pp. 225-226, plate 10, figs. 15, 16) where short, deep, disconnected grooves on the proximal sides of the corallites seem to indicate the surfaces of the cups of the corallites. The alternating succession of the corallites gives the grooves the appearance of a broken, zigzag line. In the mature stage of the colony this line largely has disappeared (page 225). In other species of *Aulopora,* especially *A. conferta* and *A. symetrica* (page 222, Pl. 10, Figs. 10-11; page 226, Pl. 1, Figs. 7-8) the median line is a distinct feature. It seems quite possible that this indicates the congeneric origin of *Bainbridgia,* but, in the lack of material for sectioning and comparison, this cannot be known positively at this time. The specific differences of *Bainbridgia typicalis,* however, are quite apparent.

Pertinent questions of whether or not these specimens may be Hydrozoa or Bryozoa arise also. If these forms subsequently should be determined to be Hydrozoans, the median impressed line may be analogous to the virgula of some supposed Hydrozoans, as, for example, in the Graptozoa.[26]

In connection with the possible relationship of these fossils to some genus of Bryozoa, Moore[27] has pointed out that the median lamina is not unlike that seen in some bryozoans, but in that group the new zooecia arise from the lamina, a mode of increase not evident in these specimens.

Another interesting feature of these fossils lies in their close similarity to several of the genera of the Auloporidae, particularly *Ceratopora* and *Cladochonus.*[28] It has not been observed entwined around a crinoid stem as in the growth of *Cladochonus.* Its most distinctive contrasts with other genera of American Auloporidae are in its lateral gemmation with the corallites in a common plane, the regular spacing between the corallite apertures, and the deeply embedded position of the corallites within the coenenchyma. Its infrequent branching perhaps should be noted, but in the fragmental material of the collections, the branching of several stalks in a common plane has been noted (Pl. 3, Fig. 6).

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24 Dr. H. W. Scott has observed in some specimens not illustrated in this paper a few cross folds or lamellae which may be perisarcal structures.

25 Pocta, P., *op. cit.,* pp. 217-230.

26 Croneis, Carey, personal communication.

27 Moore, R. C., personal communication.

28 Hill, Dorothy, and Smyth, L. B. 1938—On the identity of *Monilopora* Nicholson and Etheridge, 1879, with *Cladochonus* McCoy, 1847. Proc. Royal Irish Acad. **45**:125-138, 2 plates.

Bainbridgia typicalis sp. nov.

Plate 2, Fig. 11; Pl. 3, Figs. 5-7

Description.—Slightly flattened fragments of the corallum are about 1 mm. in diameter and may attain a length of 18 mm. Corallites evenly spaced, an average number of 3 or 4 occurring in a distance of 1 cm. along one side of the corallum. Corallites narrowly elongate and conical, slightly curving, embedded deeply in the coenenchyma, although it is not apparent from the condition of the coralla how much of the corallite tubules originally was free from the corallum. Lateral budding originates from a point about midway in the body of the parent, or, in some instances, from near the distal point (Pl. 3, Figs. 6-7). Tabulae and mural pores not observed, but slight ridges in the calyxes, possibly rudimentary septa, occasionally present.

Remarks.—It has been suggested, provisionally, that these fossils constitute possibly a new genus of the Auloporidae.[29] Morphological resemblances both to cyclostomate bryozoans and to other genera of the Auloporidae are quite striking. In general habit of growth, this species is somewhat similar to *Hederella,* but in its non-parasitic character it is distinct from that genus.[30] It seems apparent that the systematic relationships of these and of other forms of Silurian Auloporoids discussed in this paper are as involved as in later Paleozoic Auloporidae.[31]

In respect to mode of gemmation and in corallite structure, this genus resembles somewhat the Devonian genus *Cladochonus* (formerly, *Monilopora*). In that genus the origin of the new corallite from a point near the calyx rim of the parent is analogous to the mode of reproduction in this species, except the fission point is enveloped in the coenenchyma. In *Cladochonus* the fission point is in a free tubule.[32] In *Cladochonus crassus* (McCoy) the entire cavity of the corallite is open, a condition apparently shown, also, in the narrowly conical cavities of the corallites in this species.[33] (Plate 3, Fig. 7). The analogies in reproductive habit in this species and in *Cladochonus,* with other resemblances in closely similar Bainbridge forms (see description following), lead to the suggestion that possibly these Silurian forms stand in the ancestral line of closely related Devonian species.[34]

In some fossils closely related to *Cladochonus crassus* (McCoy) the impressed longitudinal line, as in this species (page 394), also is present. (U.

29 Ball, J. R., 1933—*Bainbridgia typicalis,* a new genus and species of Siluric Auloporidae. Pan-Amer. Geol. **59**:239-240.

30 Moore, R. C., personal communication.

31 Fenton, M. A., and Fenton, C. L. 1937—*Aulopora*: a form-genus of tabulate corals and bryozoans. Amer. Mid. Nat. **18**:109-115.

32 Grabau, A. W., 1899—Moniloporidae, a new family of Paleozoic corals. Proc. Boston Soc. Nat. Hist. **33**:142, pl. 2, fig. 2.

33 Nicholson, H. A., 1879—On the structure and affinities of the "Tabulate Corals," of the Paleozoic Period. Pp. 223-225, fig. 32. See also Hill and Smyth, *op. cit.* pl. 23.

34 Croneis, Carey, personal communication.

S. Nat. Museum, *Monilopora* cf. *crassa*, 41, 202).[35] In the Mississippian species, however, the impressed line does not appear to be the projection of a plane separating parallel lines of growth as suggested in *Bainbridgia* (Plate 3, Figs. 5-7).

Occurrence.—Weathered material near the top of the Bainbridge formation, hillside southwest of Camp Wrather, Ste. Genevieve County, Missouri: weathered shales and limestones of the *Pisocrinus* zone, St. Marys road, about 2¼ miles southeast of Ozora, Missouri: upper part of the Bainbridge formation, type section, NW¼ sec. 24, T. 32 N., R. 14 E., Cape Girardeau County, Missouri.

Types: Genoholotype, No. 37782, Walker Museum, University of Chicago, fragment of corallum; paratypes, No. 34518, Walker Museum, University of Chicago, fragments of coralla. (Types by Monotypy).

Family MONILOPORIDAE Grabau

Genus *Cladochonus* McCoy

Cladochonus McCoy, Ann. Mag. Nat. Hist., 20: 1847: 227.
Monilopora Nicholson and Etheridge, Geol. Mag. 6: 1879. Dec. 2, pp. 289-296, pl. 7, fig. 2.
Cladochonus and *Monilopora*, Girty, G. H., Jour. Geol. 33, 1925: 19-27.
Cladochonus McCoy, Hill and Smyth, Proc. Royal Irish Acad. 45, 1938: 125-138, 2 plates, 22 figures.

Cladochonus ? siluriensis sp. nov.

Plate 3, Figs. 8-11, 14

Description.—Corallum compound, small, commonly free, but with portions occasionally entwining the stem of a crinoid: corallites regularly alternate in the free coralla or somewhat irregularly grouped on surfaces of attachment. Corallites increase by lateral gemmation, the origin point of the new corallite just below the calyx rim of the parent. In the free coralla the corallites are widely spaced, from 3 to 5 mm. apart, but they are from 2 to 3 mm. apart where coralla entwine crinoid stems. Bases of corallites slightly embedded, the tubes mostly free, expanding slightly from the bases. Calyxes broad and shallow, but slightly protruding, the calyx elongate in the direction of axial growth in the corallum. Corallite walls thick, infrequently divided near the base in cross section by irregular, wavy lamellae which trend nearly parallel with the walls and which form a somewhat open, lamellar structure. Tabulae and septa lacking. Walls externally are generally smooth, but in some of the interlocked tubes there are annular lines or wrinkles.

Remarks.—This coral is found on a hill near Camp Wrather and occurs near the top of the Bainbridge formation. It is associated with *Bainbridgia typicalis* and *Bordenia savagei* and with other possible genera and species of Auloporoid corals.

35 The writers are indebted to Dr. R. S. Bassler of the U. S. National Museum for the loan of several species of *Romingeria*, *Ceratopora* and *Monilopora* (now called *Cladochonus*) for comparative study.

In the broadly expanded opening of the visceral chamber, bounded by thick walls with tabulae lacking, and in its habit of attachment to crinoid stems, this coral closely resembles *Cladochonus* McCoy.[36] In the thick walls of *Cladochonus* there is a distinctive reticulate structure or tissue which is regarded as a diagnostic character of that genus.[37] The reticulate structure has not been observed as characteristically present in the Missouri Silurian specimens. In its place the only distinctive wall structure apparently present is the slightly lamellar effect noted above.

In some specimens, however, both the beginning of cystose structure and what may be trabeculae, as described by Grabau[38] in *Ceratopora* may be present. The few projections into the visceral chamber, here interpreted as trabeculae, seem too irregular and too few in number to constitute the trabeculae of *Ceratopora*. Inasmuch as many of the specimens exhibit the habit of entwining crinoid stems, common in *Cladochonus*, this species is tentatively assigned with question to that genus. Probably, habit of attachment, alone, is not in itself of much importance in generic determinations. Although the characteristic features which would place this species unmistakably with *Cladochonus* have not been observed, clearly, there does not seem to be sufficient evidence assembled at present to warrant its inclusion in another genus. Suggestively, in the free growth of its coralla tubes, in the featureless nature of the visceral chambers, and in its habit of entwining crinoid stems, it possesses Cladochonoid characteristics. The lack of further distinctive features of that genus may be related to the more primitive aspects of a Silurin coral.

There are close resemblances in this species to *Bainbridgia typicalis* sp. nov., and to the corals of Auloporoid facies from the Bohemian Basin.[39] The gradual expansion of the corallite in its line of growth is about the same in this species as it is in *Bainbridgia typicalis*. However, in that species the corallite is deeply embedded in the coenenchyma, but in this one the corallites are entirely free. Moreover, the individuals are slightly more robust and rounded than in *B. typicalis*, the corallites are not restricted to a common plane as in that species, and the median impressed line is not present.

The similarity between this species and some of those described by Pocta is more apparent in *Aulopora crassa*[40] than in any of the others. But in *A. crassa* the constriction at or near the base of any corallite is quite pronounced, but it is not apparent in this species. *A. crassa* is strikingly marked by slight annular ridges, but the surfaces of this species are smooth.

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36 In a recent paper Hill and Smyth have shown that the genus *Monilopora* is synonymous with *Cladochonus* McCoy. (See citation, page 397, and again in the restricted synonymy preceding this description). Most of the references in this discussion are to the writings of Nicholson, Nicholson and Etheridge, and Grabau. In study of thin sections, however, the observations of Ball are in close agreement with those recorded by Hill and Smyth.

37 Nicholson H. A., *op. cit.*, pp. 224-225.

38 Grabau, A. W., *op. cit.*, pp. 414-415.

39 Pocta, P., *op. cit.*, p. 223.

40 Pocta, P., *op. cit.*, p. 223, fig. 2, pl. 10.

Resemblances other than those noted previously, (page 398) to the genus *Ceratopora* are not impressive in this species. Only a slight suggestion of the wall structure in *Ceratopora* has been noted so that the wall structure neither of *Ceratopora* nor of *Cladochonus* is strikingly developed. *Ceratopora,* with but few exceptions,[41] has not exhibited the habit of attachment to crinoid stems nor to other objects. The corallites of this species are not as robust and do not have the strong annular markings of *Ceratopora jacksoni* Grabau, nor the longitudinal striations of that species.

Occurrence.—Weathered material near the top of Bainbridge formation on hill near Camp Wrather, Ste. Genevieve County, Missouri. Also, *Pisocrinus* beds, St. Marys Road, 2¼ miles southeast of Ozora, Ste. Genevieve County, Missouri.

Types: Syntypes No. 34519, Walker Museum, University of Chicago, weathered fragments of coralla. Syntype, No. 45191, Walker Museum, University of Chicago, fragment of corallum entwined about crinoid stem.

41 Grabau, A. W., *op. cit.*, p. 416.

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EXPLANATION OF PLATES

FIGURES

PLATE 1

1–8. *Bordenia savagei* sp. nov.

1. Calyx view well weathered specimen, ×2. (Paratype, No. 45189, Walker Museum, University of Chicago.)
2. Well preserved solitary corallite, ×2.
3. Corallite with tabulae well exposed by weathering. ×2.
4. Solitary corallite, showing a few peripheral dissepiments.
5. Corallum, with reproduction by fission showing in the two corallites in addition to the parent individual. ×2. (Holotype, No. 34516, Walker Museum, University of Chicago.)
6. Calyx and lateral views, with fission scar at base of corallite. ×2.
7. Specimen with tabulae exposed possibly in consequence of fission, as well as weathering. ×2.
8. Corallite showing tendencies towards amplexid developments.

FIGURES

PLATE 2

1–2. *Bordenia savagei* sp. nov.

1. Composite corallum with slight development of epithecal wrinkling in left corallite. ×2. (Paratype, No. 2293, Paleontological Museum, Northwestern University.)
2. Thin-section from a compound corallum, cutting two buds in the corallite to the upper left. ×2.

3–6. *Laccophyllum petaloides* sp. nov.

3. Calicular and lateral views of a specimen approximating average size, with opening of the aulos well exposed. ×2. (Paratype, No. 45188, Walker Museum, University of Chicago.)

4–5. Calicular and lateral views of holotype, ×2. (Holotype, No. 34511, Walker Museum, University of Chicago.)

6. Calicular view of petaloid aspect caused by the paired septa, ×2; section of this specimen shown in text-figure 2. (Paratype, No. 45187, Walker Museum, University of Chicago.)

7–10. *Ditoecholasma saffordi* sp. nov.

7. Thin-section cut just below the calyx of a large-sized mature specimen. ×4.

8–9. Calicular and lateral views of holotype, showing usual proportions of corallum. ×2.5 (Holotype, No. 39352, Walker Museum, University of Chicago.)

10. Longitudinal thin-section, showing streptocolumella and tabular development. ×2.

11. *Bainbridgia typicalis* gen. and sp. nov. Fragment of corallum, ×6. (Genoholotype, No. 37782, Walker Museum, University of Chicago.)

FIGURES PLATE 3

1–4,

12. *Striatopora spiralis* sp. nov.

1. Corallum attached to crinoid stem, along with Auloporoid coral, possibly *Cladochonus*, ×2. From the orientation of the corallites on each side of the crinoid stem, it may be suggested that the corallum extended horizontally from the stem.

2. Branching corallum, somewhat flattened, ×2. (Paratype, No. 34520, Walker Museum, University of Chicago).

3. Corallum extending along and entwining a crinoid stem, ×2.

4. Corallum, with some of the calyxes distinctly showing the longitudinal ridges, possibly rudimentary septa. ×2. (Holotype, No. 45190, Walker Museum, University of Chicago).

12. Corallum attached to *Laccophyllum*, ×2.

13. A corallum with something of the flattened structure of *Bainbridgia typicalis*, but less flattened, and without the impressed median line.

5–7. *Bainbridgia typicalis* sp. nov.

5. Fragment of corallum, ground to show incomplete transverse process, ×6.

6. Fragment of corallum longitudinally sectioned, showing branching of coralla and strongly impressed median lines. ×6.

7. Fragment of corallum longitudinally sectioned, with parallel trend of corallites, lateral gemmation and median plane or impressed line. ×6.

8–11,

14. *Cladochonus ? siluriensis* sp. nov.

8. Fragment of corallum with deep calyx in lower corallite, ×2. (Syntype, No. 34519, Walker Museum, University of Chicago.)

9. Fragment, typically free corallum, ×3. (Syntype, No. 34519, Walker Museum, University of Chicago.)

10. Fragment of corallum, ×3. (Syntype, No. 34519, Walker Museum, University of Chicago.)

11. Corallum fragment typically coiled around crinoid stem, ×2. (Syntype, No. 45191, Walker Museum, University of Chicago).

14. Fragment entwined in spiral fashion around a crinoid stem; A section of one coiled specimen shows occasional trabeculae (?).

FIGURES PLATE 4

1–5,

7–10. *Laccophyllum petaloides* sp. nov.

1–4. Camera lucida drawings from a single specimen, showing changes in the septal pattern from the close of the brephic to the beginning of the ephebic stages, ×7.

5. Camera lucida drawing, showing structure of aulos and tabulae, ×7.

7–10. Camera lucida drawings from a single specimen, showing septal pattern in ephebic and gerontic stages, ×7.

6. *Ditoecholasma saffordi*, sp. nov. Camera lucida drawing showing typical ephebic septal arrangement.

PLATE 1

PLATE 2

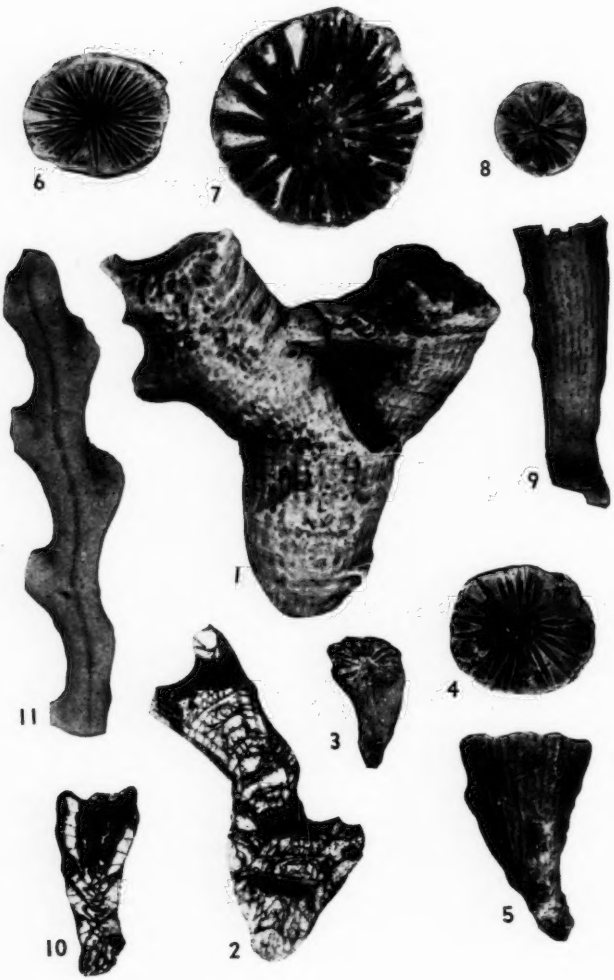


PLATE 3

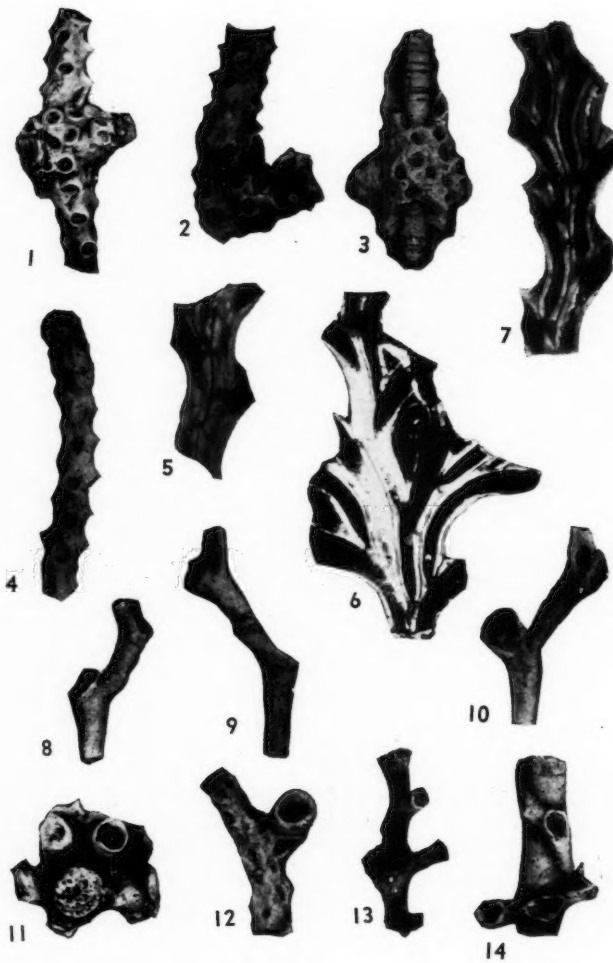
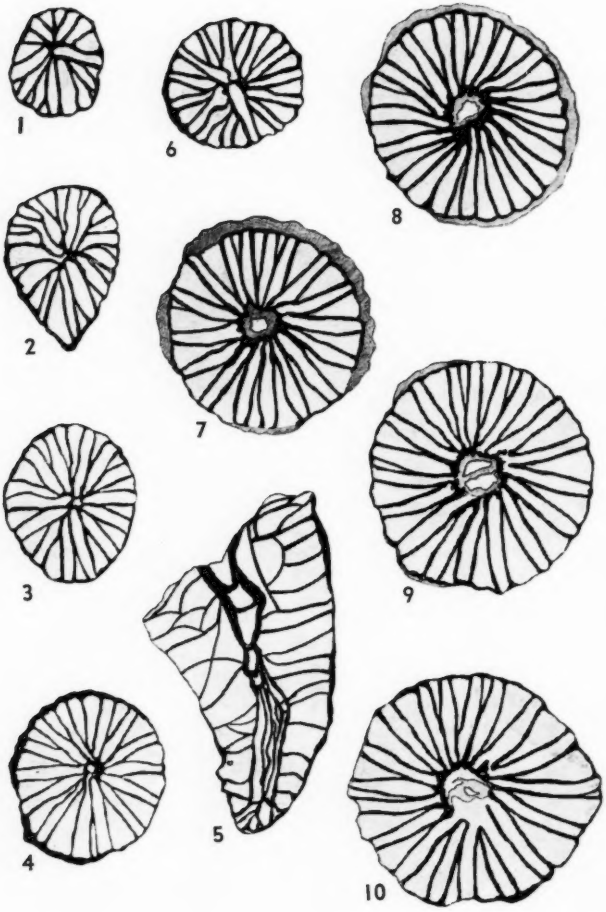


PLATE 4



New Species of Silurian Dalmanites from Southeast Missouri

John R. Ball and David M. Delo

The Silurian strata of southeast Missouri have been grouped into the following formations:

Niagaran series	Bainbridge formation (Unconformity)
Alexandrian series	Brassfield limestone (Unconformity)
	Edgewood limestone (Cyrene member) (Unconformity)
	Girardeau limestone
	Orchard Creek shale

All the species described in this paper, with the exception of *Dalmanites croneisi* sp. nov., have been collected from the Bainbridge formation. *Dalmanites croneisi* has been taken from the upper strata of a gray to pink, dense to coarsely grained crinoidal limestone which is regarded as part of the Brassfield limestone of Missouri.

This facies locally resembles both the Brassfield limestone of Ohio and Indiana and the St. Clair limestone of Arkansas and Oklahoma. Strata below the pinkish crystalline beds contain a typical Brassfield fauna including *Orthis flabellites dinorthis, Triplecia ortoni* and *Illaenus daytonensis.* Another characteristic Brassfield trilobite, *Illaenus ambiguus,* also occurs in the same horizon with *Dalmanites croneisi.*

Dalmanites croneisi appears to be identical with an undescribed species which occurs in the St. Clair limestone of Arkansas. Its occurrence in Missouri is in a horizon where Dunn[1] has found that the Foraminifera include Osgood forms almost identical with those secured by him at Joliet, Illinois, and elsewhere. *Illaenus ambiguus* likewise has been reported from the pink crinoidal beds of Oklahoma. where Cram[2] has discovered a St. Clair fauna. A coral which compares with the Brassfield *Enterolasma geometricum* (Foerste) occurs also in the Missouri Brassfield, in the pink crinoidal beds.

It thus appears that the pink, crystalline beds of the Missouri Brassfield, although containing a few typical fossils of that horizon, have some which show Osgood affinities as well. The evidence is as yet insufficient to support a definite conclusion, but some of the upper strata of the Brassfield in Missouri ultimately may be placed in the Clinton group.

Although fragmentary trilobites are fairly numerous in the Bainbridge formation, few well preserved specimens are found. *Dalmanites* is associated with species of *Goldius, Proetus, Metopolichas, Encrinurus, Calymene, Homalonotus, Cheirurus* and *Sphaerexochus.* The described species differ in general from other *Dalmanites* found elsewhere in strata of approximately the same

1 Paul Dunn, personal communication, February 10, 1939.
2 Cram I., *Oil and Gas in Oklahoma, Cherokee and Adair Counties:* 549, 1930.

age. Species of *Dalmanites* are found in the St. Clair limestone of Arkansas, the Waldron shale of Indiana and contemporary strata of Tennessee, the Niagaran dolomites of Indiana, Illinois and Wisconsin, and in the Silurian strata of Oklahoma. Almost all species from these localities have prominent caudal spines, but most of those of the Bainbridge formation appear to possess short spines or to lack them entirely. A second distinguishing feature is the coarseness of ribs in the Bainbridge species.

There is one species in the Bainbridge formation, however, which is entirely unlike the others because it is large and highly ornamented. It may be conspecific with *Dalmanites verrucosus* Hall, but the specimens are too poorly preserved for accurate comparison. The other species of the collection resemble more closely those of the basal Devonian of Missouri (Bailey limestone), Oklahoma (Haragan), and western Tennessee (Olive Hill).

Prior to 1927 the senior author[3] had collected and had designated, without published description, some of the Bainbridge *Dalmanites* as new species. More recently, the junior author has restudied the specimens in connection with his work on the Phacopidacea and has rewritten the descriptions. It seems desirable, therefore, to publish these descriptions as a unit rather than to include them with other trilobites of the Niagaran and Alexandrian species of southeast Missouri. All types are in the Walker Museum, University of Chicago. A few topotypes are in the geological museums of Northwestern University and Knox College.

Dalmanites missouriensis sp. nov.

Fig. 1

Description.—The cephalon and thorax are unknown. The pygidial width is about twice the length; margins are uniformly curved; terminus sub-angular, somewhat upturned. Rachis of moderate width, tapering rapidly and uniformly to a point; terminus merging with a sub-angular ridge which crosses the posterior border. There are 8 or 9 rachial annulations and 6 or 7 pairs of ribs which are asymmetrical, unfurrowed, and about as wide as the intervening grooves. They die out against the border by absolescence of the grooves. Surface without conspicuous ornamentation. Preservation prevents determination of whether or not a terminal spine is present.

Dimensions.—Maximum width of pygidium in holotype, 26 mm.; maximum length, 13 mm.; maximum width, rachis, 6 mm.; maximum length, rachis, 11.7 mm.

Holotype.—34654, Walker Museum, University of Chicago. A mold of a complete pygidium which does not show the terminal spine.

Occurrence.—Bainbridge formation, Niagaran series, Little Saline Creek, Ste. Genevieve County, Missouri.

Remarks.—Although the holotype is poorly preserved, the pointed rachis which continues as a subangular ridge and the small number of ribs differentiate it easily from related species. The pointed rachis distinguishes it from other species of *Dalmanites* in the same formation, as does the terminal

3 Ball, John R., *The faunas of the Brassfield and Bainbridge limestones of southeastern Missouri*, University of Chicago abstracts of theses: 264, 267-268, 1927.

ridge. It also differs from *Dalmanites bainbridgensis* sp. nov. in the narrower ribs, and from *D. salinensis* sp. nov. in the somewhat more angular ribs and wider grooves.

Dalmanites bainbridgensis sp. nov.

Figs. 3, 4; 6, 7.

Description.—Cephalon and thorax unknown. Pygidium triangular; margins sub-sinuous, border narrow; terminal spine broadly triangular, not acute, slightly upturned. Rachis low, gently tapering, blunt behind, with narrow interruptetd cross grooves; composed of 9 or 10 annulations and a short non-annulated terminus. It equals slightly more than two-thirds the total length. There are 7 pairs of ribs, exclusive of the anterior half-rib, which becomes larger distally. Ribs are very asymmetrical, with an almost vertical posterior slope which makes them appear widely separated; they curve gently and die out on the narrow border. The ends of the posterior ribs are almost even with the rachial terminus. The surface appears to be smooth.

Dimensions.—Maximum width of pygidium in holotype, approximately 36 mm.; length, 27 mm.; maximum width, rachis, 10.5 mm., approximately; length, rachis, approximately 20 mm. Maximum widths, 3 pygidia of paratypes, 27.2 mm., 30.5 mm., 30.5 mm.; lengths, 21.5 mm., 21.5 mm., 21.5 mm. Maximum widths, raches, 8 mm., 8 mm., 8 mm.; lengths, raches in 3 pygidia (paratypes) 16 mm., 17 mm., 18 mm.

Holotype.—No. 34653, Walker Museum; an almost complete weathered pygidium without test. *Paratypes.*—Nos. 34652 and 45183; two incomplete pygidia with tests; *paratype* No. 34651, W. M., one complete pygidial cast.

Occurrence.—Holotype, Bainbridge formation, Little Saline Creek, Ste. Genevieve County; paratypes Nos. 34652 and 45183, Bainbridge Creek, Cape Girardeau County, Missouri. Paratype No. 34651, Little Saline Creek, Missouri.

Remarks.—It is unfortunate that the types do not show the true nature of the terminal spine. In all specimens except the holotype the terminus is broken a short distance behind the end of the rachis and the proportions of this portion of the pygidium give no clue to its length. The holotype shows a rounded terminus which is not a spine in the strict sense, but the end of the process is broken and it seems plausible to suppose that complete specimens should show a short sharp spine.

This species differs decidedly from the Silurian dalmanitids of Arkansas and Indiana in the nature of the ribs. Their coarseness and pronounced asymmetry are highly distinctive.

Dalmanites salinensis sp. nov.

Figs. 5, 9

Description.—Cephalon and thorax unknown. Pygidium broadly triangular, narrowly rounded behind; border very narrow; width to length as five to three. Rachis narrow, uniformly tapering, very narrow terminally, equalling about three-fourths the total pygidial length; composed of 10 annulations and a very short non-annulated terminus. There are 8 pairs of angular, asymmetrical, unfurrowed ribs in addition to the anterior half-rib; they are well separated,

very gently curved through the proximal two-thirds and curved backward throughout the distal third. The anterior ribs (on casts) are as wide as the grooves, but the posterior ribs are narrower than the grooves. With test in place the anterior ribs are wider than the grooves and the posterior are about the same in width. All reach almost to the margin and the posterior ones extend backward farther than the rachial terminus. Surface without prominent ornamentation.

Dimensions.—Maximum width of pygidium in holotype, 22 mm.; length, 15 mm.; maximum width, rachis, 5.2 mm.; length, 10.9 mm.

Holotype.—No. 34655, Walker Museum, University of Chicago, a complete pygidium with test. *Paratype.*—No. 45184, W. M., a complete pygidial test.

Occurrence.—Holotype, Bainbridge formation, Bainbridge Creek, Cape Girardeau County. Paratype, Little Saline Creek, Ste. Genevieve County, Missouri.

Remarks.—This species bears a superficial resemblance to specimens of *Dalmanites bainbridgensis* sp. nov. with the terminal spine missing, but differs in the unfurrowed ribs, which are less asymmetrical and more closely crowded

DESCRIPTION OF PLATE
(All figures natural size)

Fig. 1. *Dalmanites missouriensis* Ball and Delo sp. nov. Holotype, mold of complete pygidium. Bainbridge formation, Little Saline Creek, Ste. Genevieve County, Missouri. (Holotype, No. 34654, Walker Museum.)

Fig. 2. A hypostoma occurring with *Dalmanites croneisi* sp. nov. Brassfield limestone, Little Saline Creek, Ste. Genevieve County, Missouri. (No. 34693, Walker Museum.)

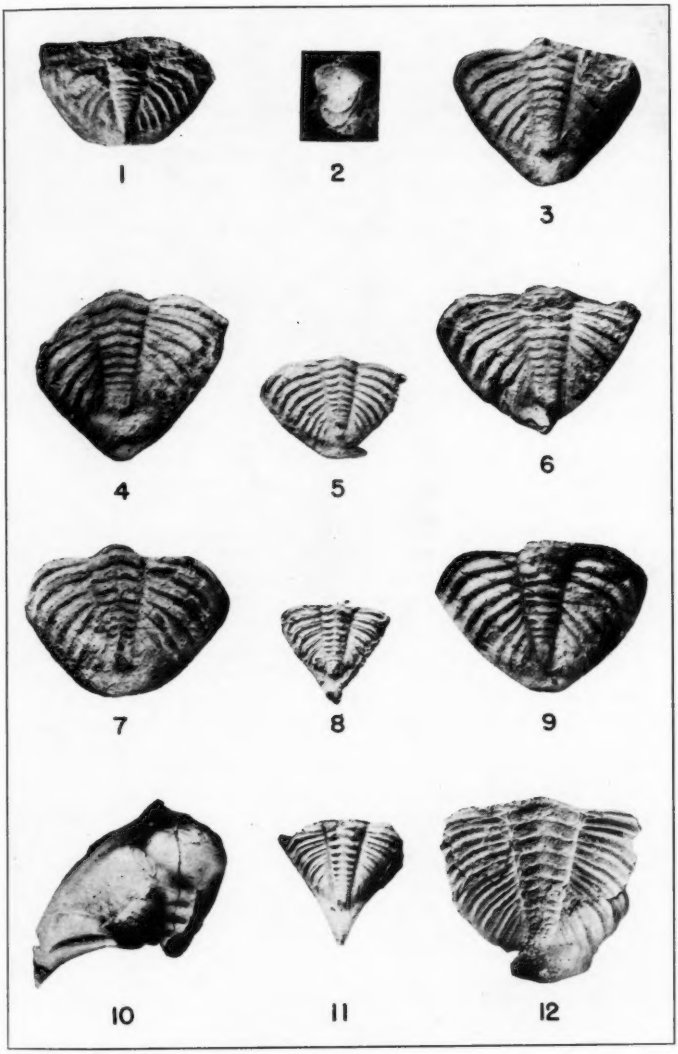
Fig. 3-4, 6-7. *Dalmanites bainbridgensis* Ball and Delo sp. nov. Fig. 3. Paratype, incomplete pygidium with fragments of test. Bainbridge formation, Bainbridge Creek, Cape Girardeau County, Missouri. (Paratype, No. 34652, Walker Museum.) Fig. 4. Holotype, almost complete weathered pygidium without test. Bainbridge formation, Little Saline Creek, Ste. Genevieve County, Missouri. (Holotype, No. 34653, Walker Museum.) Fig. 6. Paratype, incomplete pygidium with fragments of test. Bainbridge formation, Bainbridge Creek, Cape Girardeau County, Missouri. (Paratype, No. 45183, Walker Museum.) Fig. 7. Paratype, a complete pygidial cast. Bainbridge formation, Little Saline Creek, Ste. Genevieve County, Missouri. (Paratype, No. 34651, Walker Museum.)

Figs. 5, 9. *Dalmanites salinensis* Ball and Delo sp. nov. Fig. 5. Holotype, a complete pygidium with test. Bainbridge formation, Bainbridge Creek, Cape Girardeau County, Missouri. (Holotype, No. 34655, Walker Museum.) Fig. 9. Paratype, a complete pygidial cast. Bainbridge formation, Little Saline Creek, Ste. Genevieve County, Missouri. (Paratype, No. 45184, Walker Museum.)

Figs. 8, 11. *Dalmanites croneisi* Ball and Delo sp. nov. Fig. 8. Paratype, a pygidial cast. Brassfield limestone, Little Saline Creek, Ste. Genevieve County, Missouri. (Paratype No. 34688, Walker Museum.) Fig. 11. Holotype, a complete pygidial cast. Brassfield limestone, Little Saline Creek, Ste. Genevieve County, Missouri. (Holotype, No. 34689, Walker Museum.)

Fig. 10. Fragmentary cephalic cast occurring with *Dalmanites croneisi* sp. nov. Brassfield limestone, Little Saline Creek, Ste. Genevieve County, Missouri. (No. 45185, Walker Museum.)

Fig. 12. Incomplete pygidial impression occurring with *Dalmanites croneisi* sp. nov. Brassfield limestone, Little Saline Creek, Ste. Genevieve County, Missouri. This trilobite seems to have the general proportions of *D. croneisi* but is too incomplete for satisfactory identification. (No. 45186, Walker Museum, University of Chicago).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than those of *D. bainbridgensis*. The rachis is also relatively narrower, especially near the terminus, and the border is narrower.

Dalmanites croneisi sp. nov.

Figs. 8, 10-12

Description.—Cephalon and thorax unknown. Pygidium triangular; its width and length equal. Margins sigmoid, border rather narrow. Terminal spine of equal width and length, merging laterally into the border; it is acute terminally and equals one-third the total pygidial length. Rachis of moderate length, abrupt terminally, and composed of 11 to 13 annulations, the posterior 2 to 4 being indistinct. There are 7 pairs of furrowed ribs which are about as wide as the intervening grooves on casts. In each rib the posterior branch is slightly larger distally but both branches reach the rachis. The anterior ribs curve moderately throughout the distal third; the posterior are almost straight. Surface without conspicuous ornamentation.

Dimensions.—Maximum width of pygidium in holotype, 19 mm.; length, 17.5 mm.; maximum width, rachis, 6.7 mm.; length, 12.5 mm. Maximum width of pygidium in paratype, 17.5 mm.; length, 15.1 mm.; maximum width, rachis, 5.4 mm.; length, 10.5 mm.

Holotype.—No. 34689, W. M., a complete pygidial cast. Paratype.—No. 34688, W. M., a pygidial cast.

Occurrence.—Brassfield formation, Alexandrian series, Little Saline Creek, Ste. Genevieve County, Missouri.

Remarks.—Occurring with the pygidium described above is a fragmentary cephalic cast (Plate 1, Fig. 10, Walker Museum No. 45185) which shows no definitely specific characters. The eye is highly elevated, its base almost level with the glabellar surface. The anterior margin is broken, the lateral border wide. The lateral portion of the posterior margin curves backward conspicuously to the base of the genal spine, which is missing otherwise. The surface is smooth. This may represent the cephalon of *Dalmanites croneisi* sp. nov.

Species of *Dalmanites* in the Silurian strata of North America are often so similar that comparison feature by feature is necessary for accurate distinction. In this case the pygidium described has a close superficial resemblance to *Dalmanites halli* Weller from the Waldron formation of southern Indiana, and to *D. vigilans* Hall from the Niagaran of Wisconsin and northern Illinois. Moreover, it appears to be conspecific with an undescribed species in the St. Clair limestone of Arkansas.

Dalmanites croneisi sp. nov. differs from *D. halli* primarily in having pleural rib branches which are almost subequal and extend from rachis to border. In *D. halli* the posterior branch never reaches the rachis, while the anterior branch extends to the border in only the two anterior ribs.

Pygidia of *Dalmanites vigilans* differ in having straighter margins and shorter spines. There are also 2 or 3 fewer rachial annulations.

Dalmanites croneisi sp. nov. does not closely resemble any species in the Silurian strata of the Ste. Genevieve area in Missouri.

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A New Ichthyodorulite from the Geneseo Shale

(Devonian of New York)

John W. Wells

During the summer of 1939, the writer collected a number of fish remains from the Middle and Upper Devonian rocks of central New York. One of these appears to indicate an undescribed species of the characteristic Middle Devonian ichthyodorulite genus, *Machaeracanthus* Newberry, and is described below:

Machaeracanthus retusus sp. nov.

Plate 1, Figs. 1-5.

Description.—Spines of moderate size, gently curved, gradually tapering to a blunt (retuse) point distally, traversed along the middle by a prominent ridge which is nearly rectangular in section on one side of the spine (the 'upper' side) throughout its length, rounded on the other. Distally the entire 'under' side of the spine is rounded and convex. Lateral edges very sharp distally, becoming rounded proximally, the left edge (as seen from the keeled side) even becoming slightly inflated. External surfaces smooth except for the less carinated face which bears prominent longitudinal sulci separated by narrow flat-topped ridges, which terminate before reaching the distal half of the spine. Fainter sulci on the lateral edges. No trace of an internal cavity.

Dimensions.—The recovered portion of the spine is 10.3 cm. in length, 2.1 cm. wide at the proximal end (incomplete), and 0.5 cm. at the blunt distal end. An impression in the shale matrix indicated that the spine originally was at least 16 cm. long.

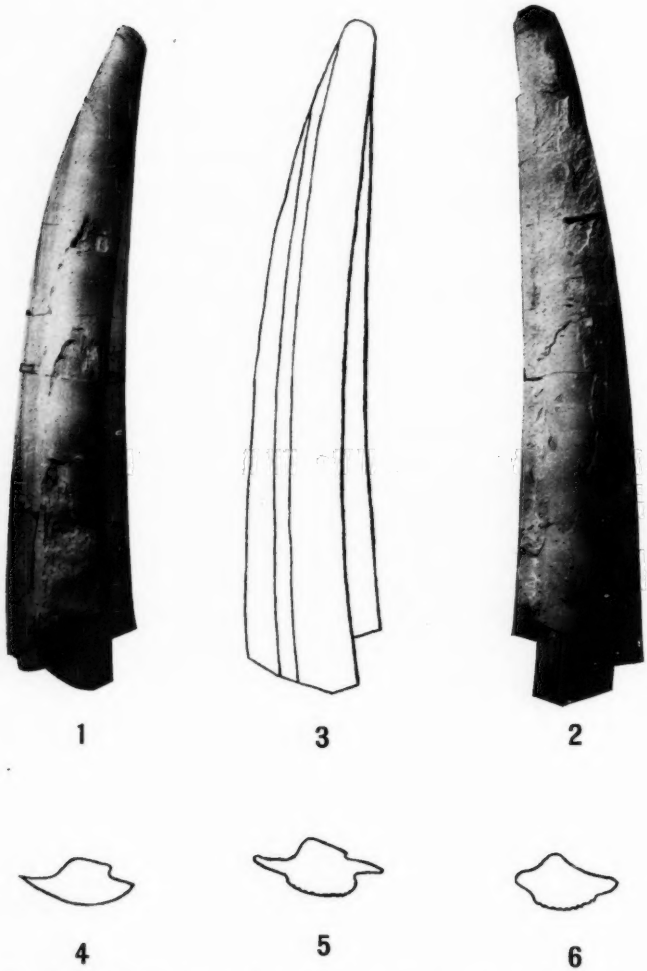
Locality and Horizon.—Found *in situ* in the lowest black shale band of the Geneseo shale member of the Genesee group about 6 inches above the Tully limestone on the north side of the gorge of Taughannock Creek, Taughannock Falls State Park, Cayuga Lake, New York. With the spine were associated small ammonoids identified by Dr. A. K. Miller as probably *Probeloceras lutheri* Clarke.

Holotype.—In the collection of the wirter.

Remarks.—The holotype specimen fortunately was nearly completely extracted from the bituminous shale matrix and reveals both sides and the tip. Unfortunately about 6 cm. of the proximal part had been exposed and lost before discovery.

The only other species of *Machaeracanthus* bearing longitudinal sulci is *M. sulcatus* Newberry 1857 of the Onondaga limestone of New York[1] and

[1] Eastman, C. R. N. Y. State Mus. Mem. **10**:84, pl. 3, f. 6, 1907.



Figs. 1-6. Fig 1. *Machaeracanthus retusus* n. sp. 'Upper' side of holotype. Geneseo shale, Cayuga Lake, N. Y. Fig. 2. Ibid. 'Under' side of holotype. Fig. 3. Ibid. Outline of 'upper' side. Fig. 4. Ibid. Outline of cross-section about 3 cm. from tip. Fig. 5. Ibid. Outline of cross-section about 9 cm. from tip. Fig. 6. *Machaeracanthus sulcatus* Newberry. Outline (reversed) of cross-secion, from Newberry, 1889. (All figs. natural size)

its equivalents in Ohio and Ontario. From this species the new spine differs in its cross-section (Pl. 1, Fig. 5). The ridge is rectangular in *M. retusus*, triangular in *M. sulcatus* (Pl. 1, Fig. 6); the lateral edges are proportionately wider in *M. retusus;* and the tip of *M. sulcatus* is acute instead of blunt. That the blunt end of *M. retusus* is not the result of wear is indicated by the sharpness of the lateral edges near the tip.

Most of the species of *Machaeracanthus* occur in the lower part of the Middle Devonian, especially in the Onondaga and its equivalents, and none are known from rocks higher than the middle of the Genesee group. The only previous record from the Genesee is by Hussakof and Bryant.[2] They mention several specimens from the Conodont limestone in Erie County, New York, a very thin, irregularly-occurring member of the group which is probably the equivalent of the much thicker Geneseo shale to the east. None of their specimens is specifically determinable, and the only one figured cannot even be associated with the present spine. All of the Conodont limestone specimens are slenderer than usual in *Machaeracanthus*.

The spine is also of interest in that it confirms the observation of Hussakof and Bryant[3] regarding *M. major* that the median ridge of the rarely-seen 'under' side terminates near the tip, the lateral edges and the ridge merging into a smooth, rounded surface (Pl. 1, Fig. 2). This is also shown in Eastman's figure[4] of James Hall's specimen of *M. sulcatus*, and is probably to be found in all well-preserved specimens of *Machaeracanthus*.

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2 Hussakof, L. & W. L. Bryant. Bull. Buffalo Soc. Nat. Sci. **12**:168, pl. 53, f. 4. 1919.

3 Ibid., 166.

4 Op. cit., pl. 3, f. 6. 1907.

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Elytha in the Cedar Valley Beds of Iowa

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In the Cedar Valley limestone occurs a group of brachiopods formerly referred to the genus *Reticularia*, but differing from Mississippian members of this genus, such as *Reticularia cooperensis* (Swallow), *R. pseudolineata* (Hall), and *R. setigera* (Hall), in several respects. Thus they tend to have a longer hingeline, a more strongly developed fold and sinus, more numerous and more closely approximated rows of spine bases and well developed radial plications, but lack double spines, as far as examination of available specimens shows. The Cedar Valley species, however, do have septa in the posterior portion of the valves. These differences are probably sufficient to remove these forms from *Reticularia*.

In most respects the Cedar Valley reticularioids are near *Spirifer fimbriata* Conrad, the genotype of *Elytha* Fredericks. There is one important difference; the spines of *Elytha fimbriata* are notably long and double. The best Cedar Valley specimens have not retained their spines, but bases show no evidence of double spines. The spine bases also are finer and more numerous and the concentric rows are closer together than those of *E. fimbriata*. It has seemed logical to place these Cedar Valley forms in *Elytha* rather than in *Reticularia*. Since they appear to differ from both genera in lacking double spines, it may be necessary to remove them later to another genus. On the other hand, additional specimens, better preserved and retaining spines, may show the spines to be double. For the present they may be regarded as members of *Elytha*.

Genus *Elytha* Fredericks 1918

Elytha subundifera (Meek and Worthen)

Plate 1, Figs. 1-5, 7-8; Plate 2, Fig. 8.

Spirifer subundifera Meek and Worthen, Geol. Surv. Ill., **3**:434, pl. 10, Fig. 5, 1868.
Reticularia subundifera Schuchert, Bull. U.S.G.S.; **87**:344-345, 1897.

Description.—Shell large, strongly biconvex, subtriangular in outline with rounded antero-lateral margins, wider than long, broadest at the midlength, the hingeline considerably less than the greatest width. Measurements of two hypotypes: length, 35.1. and 30.8 mm.; width, 41.8 mm. and 36.7 mm.; thickness, 29.6 mm. and 22.5 mm.

Pedicle valve strongly arched from beak to front with greatest curvature posterior to the midlength; moderately and regularly arched from side to side; highest in the umbonal region. Sinus originates at the beak, widening and deepening to the front margin; it is broadly concave at the bottom, bordered on either side by a large broad plication; the floor continues anteriorly to form a strong, rounded lingual extension which is nearly at right angles to the plane of the valve. Lateral slopes curve evenly and strongly from back to front and slope rapidly from the sinus to the lateral margins; they are incurved

to the cardinal margin beneath the umbo, and are marked by about 7 strong, simple, broadly rounded plications which are separated by narrow angular furrows. Umbonal region strongly convex, laterally compressed, elevated and extended beyond the hingeline. Beak strong, pointed, projecting and incurved. Area broadly triangular, flat in the lower portion, strongly curved beneath the beak, horizontally striated, and with distinct lateral margins merging with the slopes. Delthyrium higher than wide.

Brachial valve almost as convex as the pedicle, highest near the middle, gently arched along the midline from the front margin to the umbo, and strongly curved over the beak; it is more strongly arched transversely than the opposite valve. Fold strongly developed, extending from beak to front, greatly elevated above the slopes, rounded at the summit, subangular posteriorly and depressed a little anteriorly, bordered on either side by a furrow which is more elevated than the furrows on the slopes. Slopes strongly convex from back to front near the fold and more gently so near the angles, gently arched from the fold to the lateral margins, and occupied by plications similar to those on the opposite valve. Umbonal region moderately convex and slightly projecting; beak strong, blunt, slightly incurved. Area broad, low, flat, and situated in the plane of the valve

Growth lines fine, numerous, regularly spaced, finely spinose, lamellose in appearance, and about three occurring in the space of a millimeter.

Occurrence.—Cedar Valley limestone in the Atrypa bellula zone, Turkey Creek in Johnson county, Brandon, Littleton, Shellsburg, Davenport, in Iowa; Rock Island, Ill.

Holotype.—Illinois State Museum, No. 11518.

Hypotypes.—S.U.I., Nos. 6-459, 6-461, 6-462; M.A.S., Nos. 81, 120, 206, and 786.

Elytha minor sp. nov.

Plate 2, Figs. 10-13, 15-18.

Description.—Shell of medium size, unequally biconvex, subpentagonal in outline with the cardinal angles rounded, usually a little wider than long, broadest posterior to the midlength, and with the hingeline considerably less than the width. Dimensions of the holotype and of a paratype: length, 12.1 mm. and 19.7 mm.; width, 18.7 mm. and 22.7 mm.; thickness, 10.9 mm and 13.6 mm.

Pedicle valve a little more convex than the brachial, strongly arched from the beak to front with the greatest curvature posterior to the midlength, most convex in the umbonal region, strongly and regularly arched transversely. Sinus shallow, flattened or very gently concave at the bottom, indistinctly defined at the sides, obsolete in front of the beak, wide near the anterior margin and projecting into a short broad linguiform extension. Lateral slopes strongly surved from back to front near the sinus, less so toward the angles, sloping strongly from the sinus toward the extremities, incurved beneath the umbo. Plications low, simple, narrow, rounded, separated by shallow rounded furrows of moderate width, decreasing in size and distinctness away from the sinus, obsolete in the umbonal region, eight to ten on each slope. Umbo

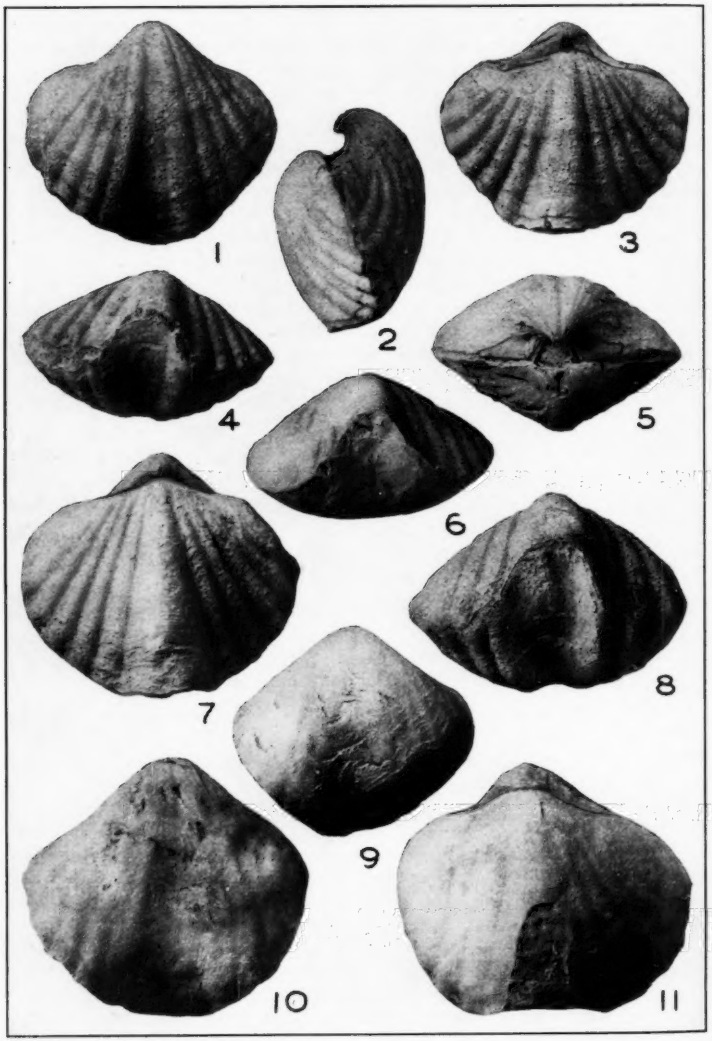


PLATE 1: Figs. 1-5, 7-8. *Elytha subundifera* (M. and W.). 1-5. Pedicle, lateral, brachial, anterior and posterior views of a hypotype from Shellsburg, Iowa, (M.A.S. 206). 7-8. Anterior and brachial views of a large example, north of Iowa City, Iowa, (S.U.I. 6-459). Figs. 6, 9-11. *Elytha johnsonensis* sp. nov. 6, 9. Anterior and pedicle views of a paratype from Johnson County, Iowa, (M.A.S. 148). 10-11. Pedicle and brachial views of a large paratype, Iowa City, Iowa, (M.A.S. 200).

elevated and projecting beyond the hingeline; beak strong, incurved, pointed, and extended. Area broadly triangular, its width half that of the shell, gently curved in the lower part and strongly curved beneath the beak, vertically and horizontally striated, and with lateral margins indistinct and merging with gentle curvature into the slopes. Delthyrium broadly triangular, and bordered by the upturned edge of the area on either side.

Brachial valve transversely subelliptical, gently arched along the fold from the umbo to the anterior margin and more strongly to the beak, strongly arched from side to side, highest near the midpoint. Fold obsolete in the umbonal region, broad and elevated at the front, broadly flattened along the summit, the sides sloping thence abruptly to the bounding furrows. Lateral slopes gently curved from the cardinal margin anteriorly and from the fold to the extremities. Umbonal region but little elevated; beak short, blunt, and slightly extended; area low and vertically striated.

Surface of both valves except the cardinal area marked by numerous somewhat lamellose concentric growth lines, more or less regularly spaced and bordered by numerous crowded spine bases.

Remarks.—This species is smaller than *Elytha subundifera*, has a lower, flatter and shorter fold, and has narrower and more numerous plications which are obsolete in the umbonal region. It differs from *Elytha fimbriata* in having narrower and in general more numerous plications, single spines, greatest width posterior to the midlength, and a flatter fold. From *Elytha undifera* from the Eifel beds of Germany it differs in having the greatest width posterior to the midlength and in having narrower, more numerous plications.

Occurrence.—Cedar Valley limestone in the Independensis zone in Johnson county, Independence, and Waverly, Iowa.

Holotype.—S.U.I. No. 6458.

Paratypes.—S.U.I. No. 6456; M.A.S. No. 210

Elytha johnsonensis sp. nov.
Plate 1, Figs. 6, 9-11.
Plate 2, Figs. 7, 9, 14

Description.—Shell large, subequally biconvex, subpentagonal in outline, wider than long, broadest at the midlength with the hingeline about half as wide as the shell, rounded at the cardinal angles, and strongly sinuate along the short and truncate front margin. Dimensions of the two paratypes, both internal molds: length, 36.1. and 26.2 mm.; width, 44.8 mm. and 36.9 mm.; thickness, 26.8 mm and 21.9 mm.

Pedicle valve strongly arched along the floor of the sinus with the curvature increasing greatly over the umbo, moderately and regularly arched transversely, and a little flattened centrally. Sinus nearly obsolete in the umbonal region, very broad toward the front, with indistinct lateral margins. Its sides are rounded and merge gradually with the slopes; it is gently and broadly concave at the bottom and projects into a long, rounded linguliform extension. Slopes gently curved from the beak to the middle of the lateral margins, but strongly curved transversely toward the sinus and the angles; inflected beneath the umbo to the cardinal margin. Plications faint, broad, gently rounded, scarcely

elevated, obsolete in the umbonal region, separated by shallow linear furrows and numbering about 7 on each slope. Umbonal region strongly elevated but slightly extended beyond the hingeline. Beak broad, pointed, much elevated above the hingeline, incurved. Area triangular, about twice as wide as high with the lower portion nearly flat and at right angles to the plane of the valve, strongly curved toward the apex, possessing indistinct lateral margins which merge with the lateral slopes. Delthyrium large, broadly triangular, about as wide as high, open to the apex. Two septa appear in the pedicle valve and a faint one in the brachial.

Brachial valve almost as convex as the pedicle, gently arched along the midline from the front margin to the umbo and more strongly thence to the beak, strongly arched transversely, highest and angular along the middle. Fold prominent anteriorly, nearly obsolete posteriorly, separated from the slopes by narrow furrows, moderately convex with the sides sloping steeply at first and then less rapidly to the slopes, shortened by the extension of the opposite sinus. Lateral slopes convex posteriorly, gently concave near the antero-lateral margins and sloping with a nearly straight profile from the fold to the lateral margin. Plications similar to those of the pedicle valve. Umbonal region gently convex; beak short and blunt, slightly projecting. Area low, nearly in the plane of the valve.

Surface of both valves marked by numerous, fine concentric lines of growth, occurring at intervals and marked along the edges by numerous fine spine bases.

Remarks.—This species resembles *Elytha subundifera,* but is larger and thinner. The area is higher and less strongly curved; the brachial valve is less strongly arched longitudinally; the sinus is broader at the front, obsolete posteriorly, and less distinctly separated from the slopes; the plications are lower and less strongly developed, and do not extend to the beaks of the valves.

Occurrence.—Cedar Valley limestone in the *Cranaena iowensis* zone at Iowa City, Linder's Boathouse, Robert's Ferry, Lost Creek, and Rapid Creek in Johnson county; a similar form comes from Randalia, Iowa.

Holotype.—M.A.S. No. 219, a pedicle valve.

Paratype.—M.A.S. No. 48, 200; S.U.I. No. 6-455, all internal molds.

PLATE 2

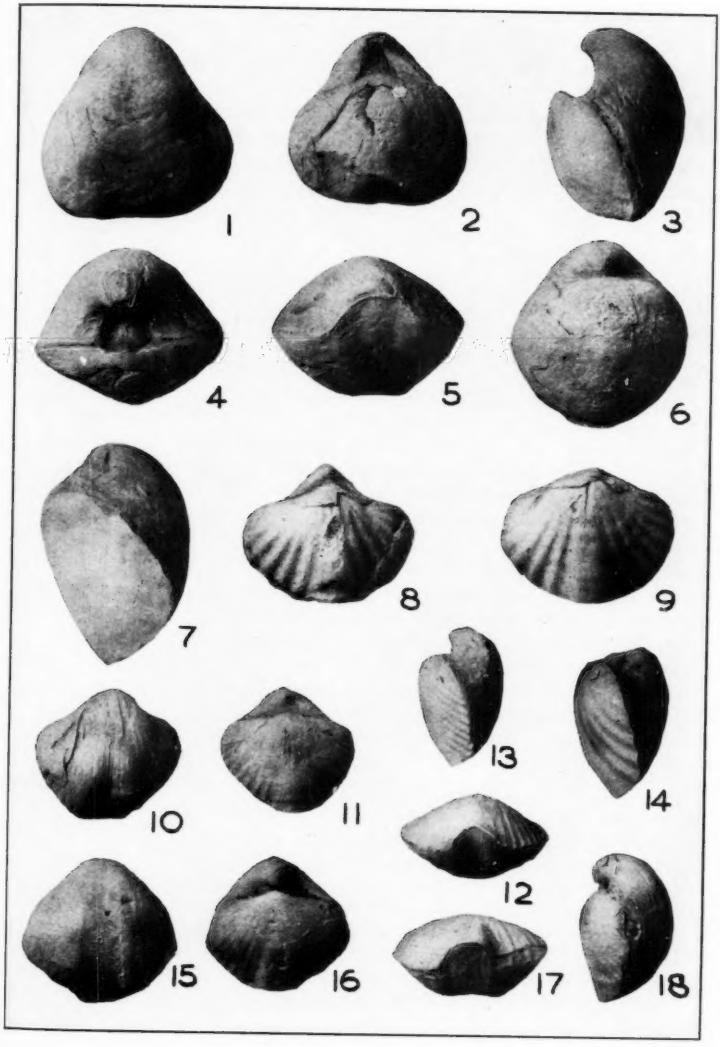
Figs. 1-6. *Elytha urbana* (Calvin). 1-4. Pedicle, brachial, lateral and posterior views of the holotpye, Iowa City, Iowa, (S.U.I. 6-464). 5-6. Anterior and brachial views of a specimen from Linn County, referred to this species.

Figs. 7, 9, 14. *Elytha johnsonensis* sp. nov. 7. Lateral view of a paratype, (M.A.S. 148). 9, 14. Brachial and lateral views of a specimen from Randalia, Iowa, (S.U.I. 6-455).

Fig. 8. *Elytha subundifera* (M. and W.). Brachial view of a specimen from the profunda zone at Brandon, Iowa.

Figs. 10-13, 15-18. *Elytha minor* sp. nov. 10-13. Pedicle, brachial, anterior and lateral views of a paratype from Independence, Iowa, (S.U.I. 6-454). 15-18. Pedicle, brachial, anterior and lateral views of a paratype from Waverly, Iowa, (M.A.S. 210).

PLATE 2



Elytha urbana (Calvin)
Plate 2, Figs. 1-6.

Spirifer urbana Calvin, Bull. Lab. Nat. Hist. Univ. Iowa, **2**:166, pl. 12, Fig. 1, 1892.
Spirifer urbanus Schuchert, Bull. U.S.G.S., **87**:408, 1897.

Description.—Shell above medium size, inequally biconvex, a little longer than wide, broadest anterior to the midlength and with the hingeline considerably less than the greatest width, subtriangular in outline with rounded antero-lateral margins and cardinal angles. Dimensions of the holotype, an incomplete specimen: length, 28.2 mm. (incomplete); width, 29.8 mm.; thickness, 22.1 mm. A complete hypotype is 35.2 mm. long, 33.2 mm. wide and 23.0 mm. thick.

Pedicle valve much more convex and larger than the brachial, strongly and regularly arched from the umbo to the front margin and more strongly over the beak, transversely flattened in the central part and strongly curved to the lateral margins, highest near the midpoint. Sinus wide, shallow, broadly flattened or gently convex along the bottom, indistinctly defined at the sides and merging gradually with the lateral slopes; it extends at the front margin. Lateral slopes strongly curved from back to front and from the sinus to the lateral and cardinal margins, incurved beneath the umbo, marked by 6 or 7 broad, low, very gently convex plications which are separated by shallow narrow furrows and obsolete on the umbo. Umbonal region prominent, greatly extended beyond the hingeline, curved. Beak strong, pointed and incurved. Area broadly triangular, about twice as wide as high, gently concave in the lower portion and strongly curved beneath the beak; lateral margins slightly angular and more or less distinct. Delthyrium very large, higher than wide, open to the apex. Interior unknown.

Brachial valve semioval with the postero-lateral margins rounded, moderately convex, highest in the middle, gently arched along the crest of the fold from the beak to the front and more strongly arched transversely. Median fold obsolete in the umbonal region, strongly developed above the remainder of the valve, and distinct at the sides. Lateral slopes gently curved from the fold to the lateral margins and from the cardinal margin to the front, bearing plications similar to those of the opposite valve. Umbonal region gently convex; beak broad, blunt, a little projecting.

Growth lines numerous, closely and uniformly spaced, occasionally very prominent; each is edged with a row of fine spine bases. From *Elytha subundifera*, *E. urbana* differs considerably; it is smaller, longer than wide and thinner; its brachial valve is more extended in the umbonal region; its fold and sinus are less strongly developed, and neither reaches the beak; the plications are not as prominent and do not extend to the beak.

Occurrence.—Cedar Valley limestone in the *Idiostroma* zone at Iowa City, Iowa.

Holotype.—S.U.I., No. 6464.
Hypotype.—S.U.I., No. 6466.

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Two New Species of Lepidostrobus from the Lower Pottsville of Orange County, Indiana

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Strobili of Paleozoic lycopods are generally abundant and well preserved in the calcareous nodules and coal balls from Europe. American workers have also found considerable *Lepidostrobus* material, but most of these specimens are preserved only as flattened impressions in shales and coal.

Coulter and Land (1911) described a petrified specimen found in a coal pocket in Warren County, Iowa. This specimen was reconsidered with additional material found in the same locality later, and described as a homosporous *Lepidostrobus* (Coulter and Land, 1921). The name *L. Coulteri* was applied to the material by Jongmans (1930), a fact which Arnold (1935) has brought to attention. The definite horizon of the coal pocket from which the material was taken was not discussed.

Scott and Jeffrey (1914) described a fragment of a petrified cone from the base of the Waverly Shale in Boyle County, Kentucky. Arnold (1935) points out that the Waverly Shale is Lower Mississippian in age rather than the suggested Upper Devonian. The name *Lepidostrobus Fischeri* was not valid because of the priority of the application of the name to some French material by Renault. Scott (1915) renamed the specimen *L. kentuckiensis*.

A partially preserved but complete lycopod strobilus from the Pottsville series of Michigan was named *Lepidostrobus Bartletti* by Arnold (1930) in order to place it on record. He suggests possible affinities to previously described European cones. In 1932 Arnold (1933) described a lycopodiaceous strobilus from the Pocono sandstone (Upper Devonian) of Pennsylvania as having Sigillarian affinities on the basis of the whorled arrangement of the sporophylls. Later (1935) he referred this specimen to the lepidostroboid group and named it *L. Gallowayi*.

Graham (1935) has discussed the occurrence of several lycopodiaceous strobili in coal balls from the McLeansboro horizon of Illinois. Complete description was impossible due to imperfect state of preservation. The relationships found between our material and the casts and petrifactions mentioned above will be discussed shortly.

The plant material to be considered here was found in the sandstone rocks of the Pocahontas group (Lower Pottsville) of Orange County, Indiana. The presence of plant fragments from the western part of that state has long been noted. Lesquereux (1884) lists ten species including seven ferns and three Lepidodendra. David White (1895) records and discusses 19 specimens of leaf and wood impressions from four quarries in the northwest part of Orange

County. Coulter and Land (1921) reported the possession of some stem fragments but no cones from the sandstones of western Indiana. Weller[1] states that extensive collections have been made from the Lower Pottsville (Pocahontas) Series and are described in a manuscript by the late David White. The two larger cone specimens which we have were obtained a number of years ago. The remainder of our material with the exception of an extremely fine cast of a branch tip of *Lepidodendron (aculeatum)* was collected recently. The entire collection was found in the several Chailleaux and Whetstone quarries about 6 miles northwest of Orleans, Indiana. The sandstone is in two stages and varies from fine to medium grain.

The upper of the two stages is the main massive body of sandstone. It is overlain by a thin underclay. In this rock the plants are rather poorly preserved and not as numerous as in the thinly bedded sandstones below. Several large fragments of fair sized trees were found. One of especial note is lying prostrate along a bedding plane and one of the branches of the first dichotomy forks four more times successively. At the second dichotomy, one branch penetrates about three feet of sandstone in an almost vertical position. Over twenty feet of the cast of this tree was exposed in relief by quarrying operations. Kindle (1896) mentions the similar occurrence of a fossil tree in a quarry of this region.

Directly beneath this massive layer, a lesser zone of thinly bedded, very fine, shaly sandstone occurs. It is underlain by a thin coal. Wanless[2] suggests that this is the coal called No. 1 in the Orange County report (Elrod and McIntire, 1876). Kindle (1896) has described the whetstone rocks in some detail.

The age of this deposit of plant material at the base of the Pottsville Series is important. The plants are dissimilar to those known to occur in Indiana, Illinois and western Kentucky, and are possibly the oldest in the interior coal basin.

The four specimens of Lepidostrobus which we have prepared for study may be divided into two rather obvious types.

Three of the specimens are of the first type. The largest and best example of the first type was only partially exposed along one side when found. Careful work with hammer and chisels in the laboratory have exposed an excellent cigar-shaped cone, about 13.5 cm. long and 2.5 cm. in diameter at the base. The tip is missing. The cellular detail has been lost through imperfect preservation as a cast, but all the external morphological features are well shown. After pictures, rubber molds and plaster casts had been made of the entire specimen, a section was cut through the cone 1.5 cm. from the base. A fortunate accident resulted in the breaking of a portion out of this lower section. This exposed some interesting structure which might only have been conjectured otherwise. The axis at the basal point of attachment is about

1 Weller, J. Marvin, Ill. Geol. Surv. — Personal communication.

2 Wanless, Harold R., Univ. of Ill., — Personal communication.

5 mm. in diameter. It tapers abruptly so that within 5 mm. of the base, the diameter is reduced to about 3 mm. In cross section at the base, at a point 5 mm. above the base, and at the broken tip of the specimen, the axis has 13 ridges visible which are the old sporophyll bases. The significance of this number is not known, but a similar condition is found in *L. Bartletti* and in the description given by Bower (1893) of *L. Brownii*. Certain other species have only 11 of these sporophyll bases or less, but there is, apparently, a rather constant number for each species.

There are, then, normally 13 sporophylls in each spiral revolution about the axis and in a longitudinal section through the cone there are between 95 and 100 such revolutions, in the known 13.5 cm. Such a number of sporangia would indicate their small size.

As in *L. Coulteri, L. Bartletti, L. Gallowayi,* and the specimens discussed by Graham (1935), the sporophylls are borne approximately at right angles to the cone axis. The sporangia are radially elongated as is characteristic of the lepidostrobus type of lycopod cone. They are borne adaxially on a pedicel, i.e., the portion of the sporophyll which is horizontal. The distal end of the sporophyll, called the lamina by Scott (1920), turns up and overlaps the ends of the next several sporangia. These laminae are rather narrow at their bases, not over 1.5 mm. wide, and are usually less than 2 cm. long. They are closely appressed throughout their length and are imbricate in appearance. Two specimens of this type of cone show the imbricate condition very well. An outstanding feature of the sporophyll is the apparent lack of any portion subtended below the horizontal plane of the pedicel. Hirmer (1927) states that a subtended portion is usually present as does Scott (1920) who adds that the form of the whole sporophyll is somewhat peltate as a result. When this condition exists, as it does in our second type of cone, a portion of the lamina is not only subtended but this part as well as the distal end of the pedicel is usually strongly thickened. The lack of the subtended portion of the lamina is not peculiar alone to our specimen. Graham (1935) discovered a similar situation in his material and states, "The lax nature of the cone and the absence of a downward projection of the lamina distinguish this from previously described species." Such a condition may exist in other species which have been described, but if so, it is neither discussed nor pictured clearly. A median nerve is very prominent on the lamina.

The sporangia, which are about eight mm. in length and slightly over one mm. in height are roughly wedge-shaped in top view. The end nearest the axis is very narrow and is generally wedge-shaped in cross-section. The distal end is rather broad and flattened. The sporangia are so crowded together both laterally and vertically that their sides are fluted by the pressure from adjoining sporangia. Due to the small size of the sporangia and the deformation present we are unable to ascertain the amount, position and mechanics of the attachment to the sporophyll. The presence of a ligule has not been proven for this type in our collections. A cross-section through the entire cone shows well the laterally compact nature of the sporangia and the vertical distortion. The drawing and photographs illustrate this point rather clearly.

A second type of cone, represented by one of the four specimens, was exposed by splitting open a rather large, cut slab of grey sandstone. The cone split irregularly through the axis and thus we have a single specimen well shown on both slabs. The cone is somewhat flattened but chiseling has revealed that the flattened diameter is about 2 cm. whereas the normal diameter is about 2.7 cm. Both ends of the cone are missing and no tapering is apparent in the 11.5 cm. which we have. Unfortunately, several small concretionary growths have either destroyed or distorted about one-half of the middle section of our specimen. As in the first type of cone already discussed, no cellular detail is visible but the general organization and external morphological features are well shown.

The axis is about 5 mm. in diameter throughout its entire length. In cross-section there are usually eleven sporophyll bases exposed as ridges which indicate the presence of eleven sporophylls for each revolution about the axis in a spiral order. The reconstruction shows 43 such spiral revolutions in the 11.5 cm. This number is less than one-half that found in the first type, although this specimen is only 2 cm. less in length. By computing this average, which agrees quite closely with the measurements taken, the sporangia are slightly more than 2.5 mm. high.

The adaxial angle of the sporophylls to the axis is slightly greater than a right angle, i.e., the distal ends of the sporophylls slope toward the lower end of the cone as much as 93° or 94°. This is accentuated by a prominent, subtended portion of the lamina and a thickened distal end of the pedicel of the sporophyll. The sporophylls at the lower end of the specimen are angled slightly more than this, possibly as a result of the release of the vertical pressure of the compacted sporangia when the lower portion was broken away. The distortion resulting from the concretionary growth in the middle of the specimen is shown by the varying angles of attachment of the sporophylls in the affected area.

The pedicels and sporangia are arched in the middle so that both the axial and distal ends are lower. The distal end is much lower because of the angle of attachment of the sporophyll to the axis. None of the descriptions of casts or petrified American cones records either the arching or the downward slanting pedicels and sporangia. Text discussions and figures by Hirmer (1927), Figs. 208 and 210 of *Lepidostrobus Brownii* and *L. Oldhamius* respectively, Scott (1920), Fig. 77 of *L. Veltheimianus*, and Solms-Laubach (1891), Fig. 25 of a different specimen of *L. Brownii* than that shown by Hirmer, indicates that these characters have been noted and considered in the European material.

The sporophyll is extremely important in this second type of cone. The broader, flattened part of the pedicel appears to be attached to the axis by a more typically stalk-like portion which is turned abruptly down along the axis and is fused to it throughout its length of one mm. This might be called a rather enlarged sporophyll base. Such a structure is not discernible in the first type of cone. The pedicel itself, i.e., the horizontal portion of the sporophyll which bears the sporangia on its upper surface, is very narrow. This feature shows well in a number of places. The pedicel is flared out broadly

at the distal end and is thickened noticeably. The lamina and the pedicel form a definite subtended portion very similar to that modelled after *Lepidostrobus Coulteri* (Coulter and Land, 1911). The lamina is 3 to 4 mm. wide at the base and 30 to 40 mm. long. It tapers gradually to a width of 1 mm. in the first 12 mm. of length, and is characteristically appressed for the lower half. The upper half of the attenuated lamina is slightly divergent and aristate in nature. This is contrasted to the closely overlapping, appressed, imbricate nature of the first type of cone described. A median nerve is definite for the length of the lamina but is not as marked as in the first type. Such a sporophyll seems to be unusual, at least in regard to length. The presence of ligules at the distal ends of the sporangia cannot be definitely shown. Some very confusing markings appear which, if liberally interpreted, may be considered as ligules.

The sporangia are closely crowded both laterally and vertically and are prominently grooved by the adjacent sporangia. In cross-section they differ markedly from those described in the first type. They are narrowed at the axial end but not wedge-shaped. At the distal end they are oblong-ovate in cross-section. The sporangium is rather broad in comparison with the pedicel, and broadly overlaps it. In adaxial view the outline of the sporophyll is generally wedge-shaped. The spores of this cone and of the first type will be discussed together.

The spores of our cones were secured by macerating the sporangia. In our first type of cone only one kind of spore was found. The average diameter of this is about 26-29 μ. A triradiate opening is present in some and absent in others. An equatorial flange is present in a few instances. Whether another type of spore exists and was not found is not known. It would be unsafe to hazard the statement that this specimen is homosporous on the negative basis of not finding larger spores. It is interesting to note that except for its larger size, *Lepidostrobus Coulteri* is very similar to our species. Spores of but one kind were found in *L. Coulteri*. The diameter of these spores is comparable to that of the spores of our specimen. Campos (1925) in describing a complete specimen, *Lepidostrobus foliaceus*, finds only one size of spore, and that measures 32 μ, which is only slightly larger than our spores. These spores are very similar to ours in general outline and in the nature of the triradiate marking. He states that his specimen is homosporous. However, Mrs. D. H. Scott (1906) had described a megaspore from a different specimen of *L. foliaceus*. Campos justifies his conclusions by a statement from Berry (1918) that different cones may produce two kinds of spores. However, if two sizes of spores are known to occur in this species, it is certainly difficult to indicate the homosporous nature of any single specimen. Only a complete, well-preserved cone such as the specimen described by Campos may be safely called homosporous.

In studying the spores from our second type of cone, the microspores are found to be practically identical with the spores found in the first type, i.e., 26-29 μ. Most of them have a definite triradiate opening. In addition, a larger spore is found sparingly, at a ratio of about 3 to 100. The size of this

larger spore, 160-170 μ, agrees fairly well with the megaspores figured by Arnold (1933) for *Lepidostrobus Gallowayi*, which measure about 150 μ. Certain definite features show clearly that the two cones are of different species. *L. Gallowoyi* has whorled sporophylls and is considerably larger.

In order to obtain the spores from our material, several techniques were tried with varying results. Sandstone is normally a poor matrix for the preservation of spores. The spores were not revealed in the sporangia when viewed through a binocular microscope using direct light. Such a condition could be expected, however, so to make sure of the presence of the spores, individual sporangia were chipped from the cones and broken into several small pieces. The most satisfactory procedure found for freeing the spores was first to allow the material to stand for about 15 minutes in hydrofluoric acid. After several washings, Schultz's solution was poured over it and allowed to stand for about an hour. This was followed with several washings in distilled water after which the material was placed in a 30% solution of NaOH (sodium hydroxide). This was allowed to stand from 2-24 hours depending on the amount of organic material present. The NaOH was then poured off and the material washed until neutralized. Without drying, "abopon", a Glyco mounting medium, which is water soluble, was added. The permanent mounts made from this are available for further study.

It is possible that the spores which we obtained were merely washed into or in some manner infiltrated among the sporophylls and sporangia before fossilization. If so, we may not have the original spores at all. This possibility exists in all material preserved as casts. Petrifactions in coal balls and concretions are less likely to be contaminated. It is interesting to note, however, that several fragments of the surrounding matrix were processed in the same manner and the presence of spores from that material could not be definitely established, whereas in the macerated material from the sporangia spores were fairly numerous. The detritus taken from the concretionary growths in the central part of the specimen of our second type of cone was found to have an abundant spore assemblage. This could be expected, since in formation the concretions disrupted the sporangia and then reincorporated them and their contents.

A rough and thickened exine, which should be found on any megaspore unless lost before preservation (Thomson, 1934) is not always evident on the megaspores from our second type of cone. Certain exterior roughenings are present in one or two spores and these resemble somewhat the megaspore figured by Arnold for *Lepidostrobus Gallowayi*.

With the discussion and criteria in mind, we feel that these cones merit a definite record in paleobotanical literature. While we do not wish to expand this literature with unnecessary new names of species, it seems desirable to give the specimens a name, even though they may lack some of the fundamental characteristics necessary for a complete description. Moreover specimens which are not given a name may easily be overlooked. An attempt has been

made to compare critically our specimens with casts and petrifactions of *Lepidostrobus* which have already been described.

The summarized type diagnoses follow:

Lepidostrobus imbricatus sp. nov.

Cone: Medium size, 13.5 x 2.5 cm., cigar-shaped not flattened, basal portion intact, tip missing. Preserved as cast in fine sandstone.

Axis: 5 mm. in diameter at base but tapers abruptly to 3 mm. throughout remainder of cone. 13 sporophyll bases prominent when viewed in cross-section. No cellular detail observed.

Sporophylls: Arranged spirally, 13 per revolution about axis and approximately 100 revolutions in 13.5 cm. Pedicels inserted at right angles to axis and about 8 mm. long to distal end where lamina curves evenly upward. No subtended or thickened portion of lamina evident. Laminae 1.5-2.0 cm. long, slender, not over 1.5 mm. wide at base, tapering gradually to sharp point, closely appressed, overlapping many laminae above, imbricate in appearance. Median nerve is prominent.

Ligule: Definite evidence lacking, possibly because of imperfect preservation.

Sporangia: Borne adaxially on sporophyll pedicel. Greatly elongated (8 mm.), wedge-shaped in top view, wedge-shaped in cross-section near axis but broadly flattened at distal end and overlapping narrower sporophyll; attachment not distinguishable. Densely crowded vertically and laterally and thus distorted.

Spores: Small (26.5 μ), triradiate openings in some; obtained only by maceration. No larger spores found in this cone.

Location and horizon: Pocahontas sandstone, lower Pottsville series, Pennsylvania system. Six miles northwest of Orleans, Orange County, Indiana; Chailleaux quarries.

Number of specimens: Three. One fairly complete cone, the type specimen, and two smaller fragments. Several traces of other cones of probably the same type are in the Paleobotanical Museum, Botany Department, University of Cincinnati.

Name of type: *Lepidostrobus imbricatus*, after the imbricate nature and appearance of the laminae of the sporophylls.

Lepidostrobus aristatus sp. nov.

Cone: Medium sized cone, 11.5 x 2.7 cm. Incomplete, both ends missing. Slightly flattened. Preserved as cast in fine sandstone. Middle of specimen distorted by growth of concretions.

Axis: 5 mm. in diameter throughout known length. 11 sporophyll bases on axis when viewed in cross-section. No cellular detail preserved.

Sporophylls: Arranged spirally, about 11 sporophylls per revolution and 43 revolutions. Adaxial angle of pedicel part of sporophylls to axis slightly greater than right angle. Pedicel 1.1 cm. long. Prominent stalk-like sporophyll bases about 1 mm. long on axis. Laminae very wide at base (3-4 mm.) and 30-40 mm. long. A portion of the lamina is subtended prominently below the horizontal plane of the pedicel and is slightly thickened. Laminae taper rather gradually from wide base to an attenuated tip, are closely appressed for the lower half but slightly divergent above. Aristate in appearance.

Ligules: Presence questionable. Indefinite structure arises from distal end of pedicel.

Sporangia: Borne adaxially on sporophylls, closely crowded. 1 cm. long, wedge-shaped in top view, narrow, but not triangular in cross-section next to the axis, broader and somewhat rectangular-ovate at distal end. Narrower pedicel is broadly overlapped by sporangia. Attachment to sporophyll appears to be throughout length by narrow band of tissue.

Spores: Two sizes of spores have been found by macerating sporangia. The smaller spores are 27 μ and the larger are 160-190 μ. Triradiate openings are prominent but no bristles are visible, the exine possibly having been destroyed.

Location and horizon: Pocahontas sandstone, Lower Pottsville series, Pennsylvania system. Six miles northwest of Orleans, Orange County, Indiana; Whetstone quarry.

Number of specimens: One specimen, exposed by splitting sandstone block. Split in half. Paleobotanical Museum, Botany Department, University of Cincinnati.

Name: *Lepidostrobus aristatus*, after the aristate nature of the attenuated, slightly divergent laminae of the sporophylls.

Acknowledgements are due to Dr. A. H. Blickle of the University of Cincinnati for advice and other services and to Mr. Frank Kroeger of the University of Notre Dame for assistance in preparing Fig. 13.

Summary

1. Several incomplete *Lepidostrobus* cones have been found along with other plant remains in the Lower Pottsville sandstones of Orange County, Indiana.

2. Diagnostic characteristics of the cone material are given and the two evident types which result are compared with other known casts or petrifactions of *Lepidostrobus*.

3. *Lepidostrobus imbricatus* and *L. aristatus* are the proposed species names for the two types of cones discussed.

4. Summarized type descriptions are given for each species.

Botany Department,
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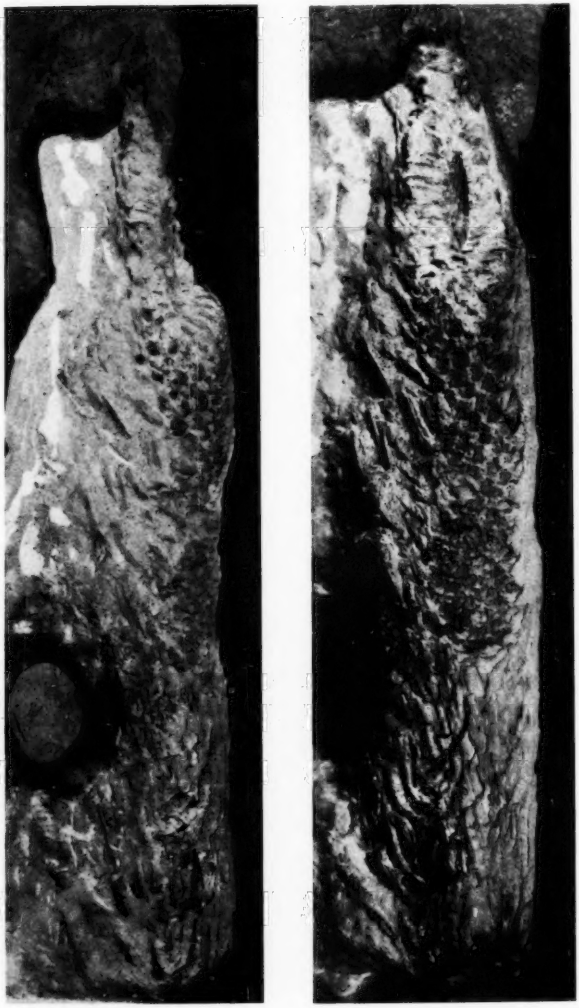
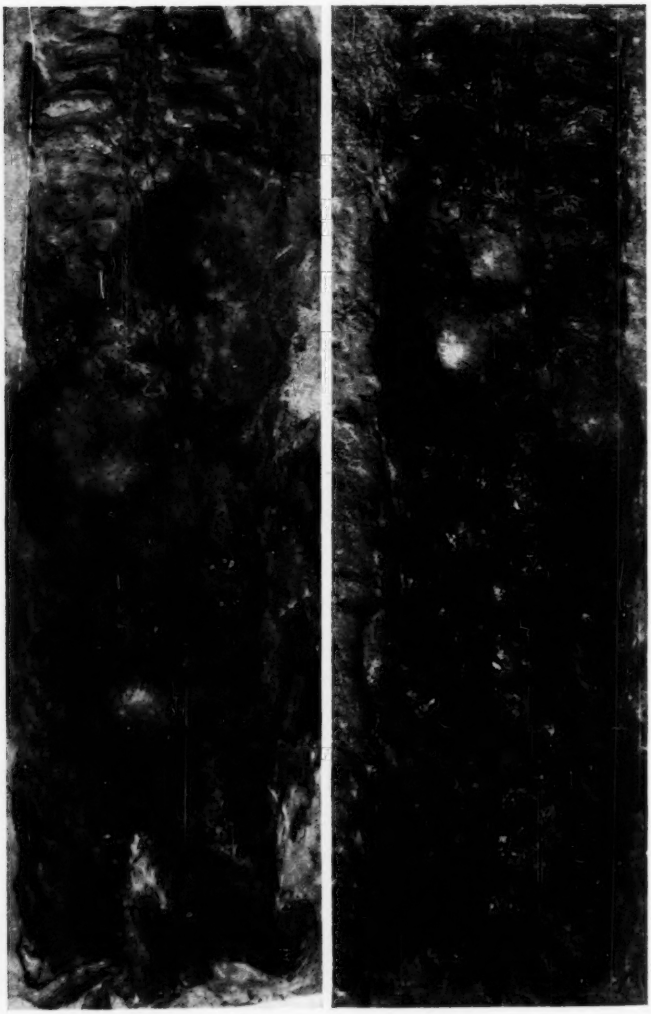
Cincinnati, Ohio.

PLATE 1



Figs. 1 and 2. Type Specimen of *Lepidostrobus imbricatus*. x1⅛.
Fig. 1. Side view. Fig. 2. Front view.

PLATE 2



Figs. 3 and 4. *Lepidostrobus aristatus* as split from rock. ×1¼.

PLATE 3

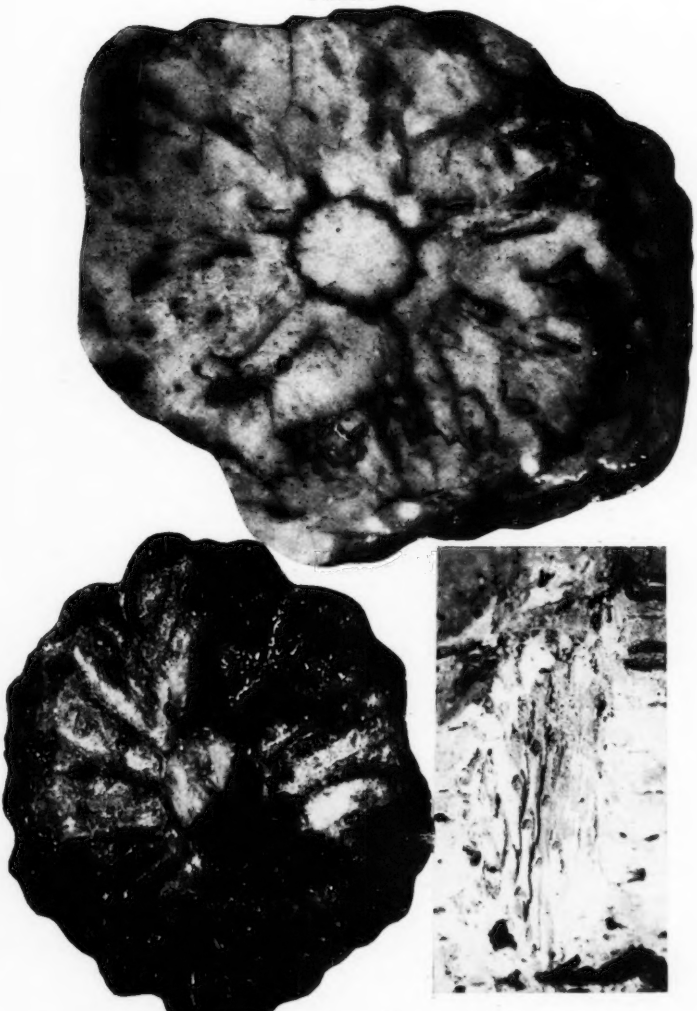


Fig. 5. Cut cross-section near base of *Lepidostrobus imbricatus* showing axis in center, with longitudinal sections through sporangia surrounded by transverse sections of erect laminae of sporophylls of lower insertion. ×5.

Fig. 6. Broken base of same cone showing clearly, the outline of sporangia. ×3½.

Fig. 7. Central axis of another specimen of *Lepidostrobus imbricatus*. ×7.

PLATE 4

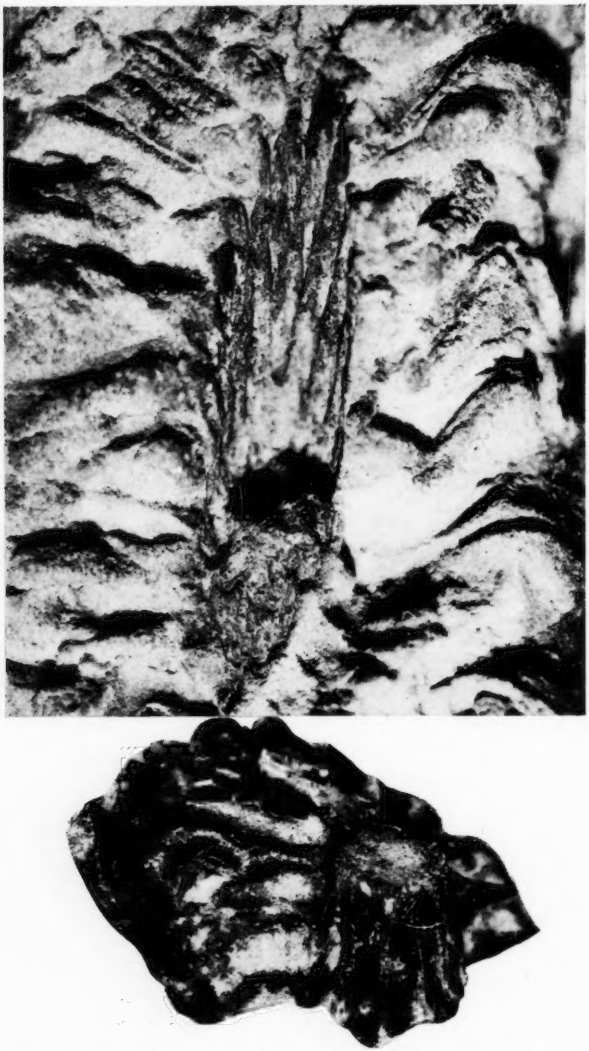


Fig. 8. Greatly enlarged section of tip of axis of type specimen of *Lepidostrobus imbricatus* showing attachment of sporophylls. ×7.
Fig. 9. Broken section of base of same specimen showing abruptly tapering axis. ×5.

PLATE 5

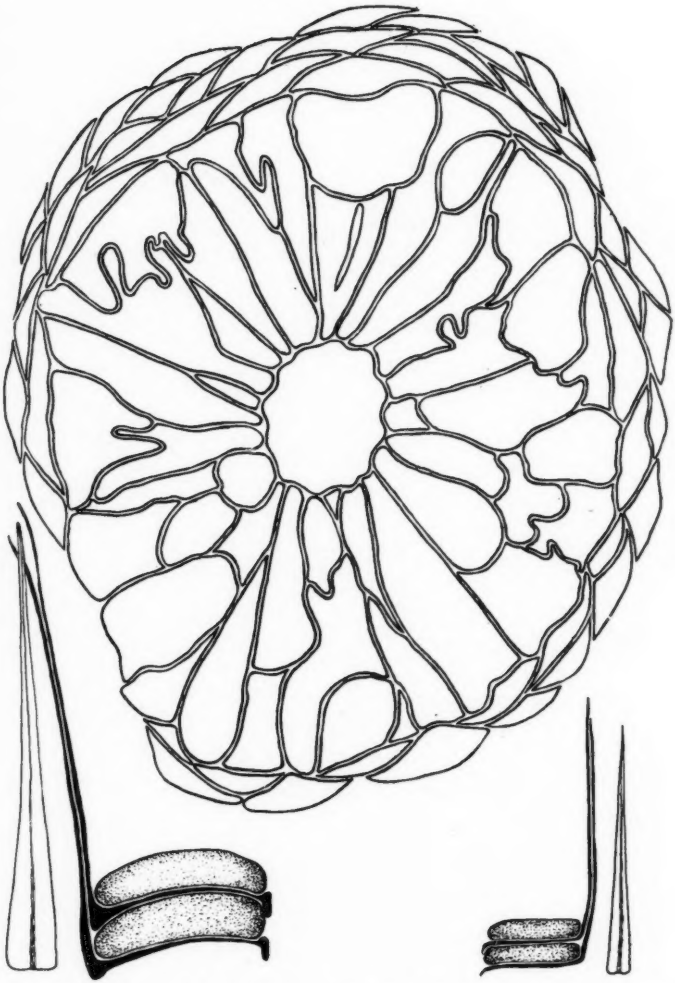


Fig. 10. Reconstruction of cross-section of axis of *Lepidostrobus imbricatus* based on Fig. 5. ×5.

Fig. 11. Enlarged sporophyll and sporangium of *Lepidostrobus imbricatus*. ×2.

Fig. 12. Enlarged sporophyll and sporangium of *Lepidostrobus aristatus*. ×2.

PLATE 6

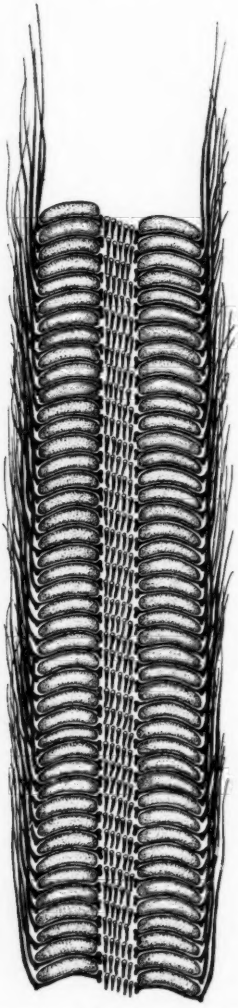
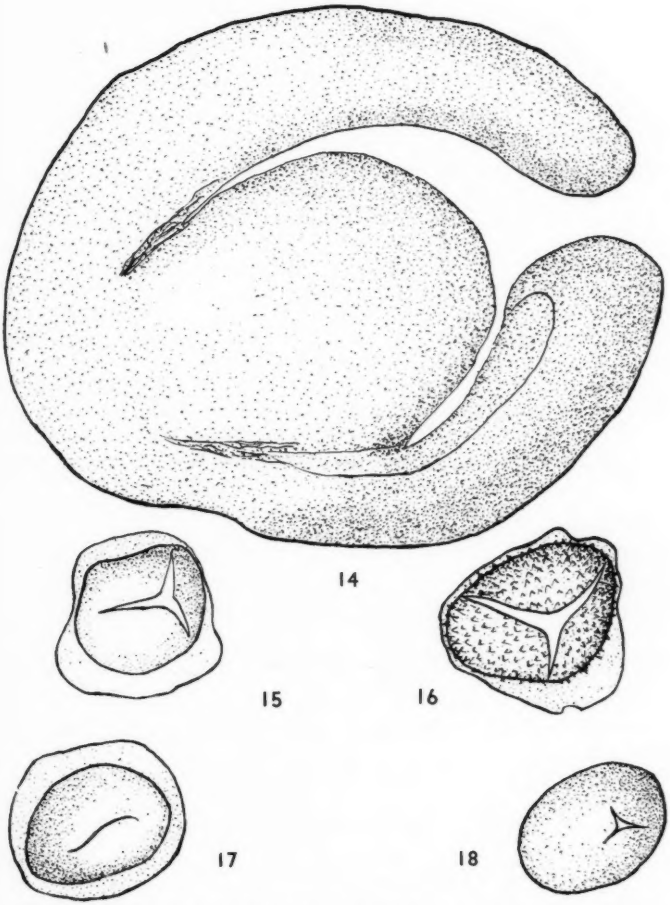


Fig. 13. Reconstruction of *Lepidostrobus aristatus*. ×1¼.

PLATE 7



Figs. 14-18. Camera lucida drawings of spores from cones showing relative proportions.

Fig. 14. Megaspore of *Lepidostrobus aristatus*. 165 mu.

Fig. 15. Microspore of *Lepidostrobus aristatus*, showing equatorial flange and triradiate opening. About 29 mu.

Fig. 16. Microspore of *Lepidostrobus aristatus* with roughened exine. 29 mu.

Fig. 17. Microspore of *Lepidostrobus imbricatus* with single slit opening. 26 mu

Fig. 18. Microspore of *Lepidostrobus imbricatus* with trace of triradiate opening. 26 mu.

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Notes on the Systematic and Ecological Implications of the Miocene Flora of Sucker Creek, Oregon and Idaho*

Helen V. Smith

The Sucker Creek flora of Malheur County, Oregon and Owyhee County, Idaho has been known since the report (10) on Lindgren's collection of 1898. Knowlton studied the collection and listed seventeen species which he correlated with the Payette flora that he had previously described from Montour and the Boise Basin, Idaho. He did not make specific determinations of most of the plants and the flora remained relatively unknown for a number of years. Chaney in 1921 collected specimens from five Payette localities, three of which were in the Sucker Creek area. He reported seventeen species not previously known from the Payette, but did not list the specimens by locality, so it is not known how many species came from Sucker Creek. In his report (7) published the following year (1922) he discussed in a general way the ecology of the plant associations represented in the Payette deposits and suggested that the association was quite similar to certain modern forests of the west. He called attention to the dominance of the genus *Quercus* and pointed out that a large number of fossils closely resemble the California live oaks, notably *Q. chrysolepis*. The abundance of such oaks and the scarcity of *Sequoia* he considered to be indicative of a dry slope habitat. He believed that the climatic conditions and topography were not unlike those of northern California and southwestern Oregon today.

Berry (5) published a list of eleven species collected by Sam Ballantyne on his ranch in the lower part of the Sucker Creek valley in Idaho, with no discussion of systematic or ecological relationships. Brooks (6) reported twenty-eight species, mostly from the vicinity of the Ballantyne Ranch. She briefly discussed the ecology of the assemblage and pointed out its similarity to modern floras. She believed the assemblage was one of mixed xerophytic and mesophytic types. Arnold (1, 2, 3) and Smith (12, 13) have added a number of species to the list of those known from Sucker Creek but neither discussed the ecological implications of the flora as a whole.

It is the purpose of this paper to bring together our present knowledge of the flora and to make further suggestions concerning its geographic and ecologic implications. It must be emphasized that this is merely a preliminary study and that a great deal more work must be done before the Sucker Creek flora can be clearly understood.. It is true that the majority of the easily recognised and more familiar species have been reported, but there remain a number of

* Papers from the Department of Botany and the Botanical Gardens of the University of Michigan no. 714.

species as yet undescribed of which the relationship to modern plants is unknown and may remain so for some time. When these are understood they will in all probability add to the list of those species now represented by species growing at great distances from Sucker Creek. Another source of confusion is encountered in trying to identify the small *Quercus* or *Castanopsis* leaves. Without implying agreement with the synonymy given by Mrs. Brooks for the Sucker Creek species which she refers to *Castanopsis,* I suspect that at least some of the leaves actually belong to that genus, although some that she would include in *Castanopsis* I consider better placed in *Quercus*.

Corresponding to over one hundred names that have been listed for Sucker Creek fossils, I believe that 58 species may be recognized.

In the compilation of the list recent suggestions on synonymy were taken into consideration. Some plants that have never been given specific names have been entirely disregarded, as have those that have been so doubtfully determined as to cause the author to question the names. A few species, such as *Quercus cognata* Knowlt. and *Q. Trainii* MacG. listed by Brooks were omitted, the first because, judging by the photograph, the specimen was too poorly preserved for certainty of identification, the second because of Mrs. Brook's own expressed doubts as to the identification of the species. Neither has been reported by other workers. Of the species enumerated I have seen either specimens or photographs of all but four species, namely *Amelanchier typica* Lesq. and *Castanea orientalis* Chaney reported by Berry (5) and *Cornus ovalis* Lesq. and *Prunus covea* Chaney reported by Brooks (6).

The Sucker Creek flora as here interpreted includes the following 58 species belonging to 37 genera and 25 families:

PTERIDOPHYTA

Equisetaceae
Equisetum octangulatum H. V. Smith

Polypodiaceae
Woodwardia deflexipinna H. V. Smith

SPERMATOPHYTA

GYMNOSPERMAE

Ginkgoaceae
Ginkgo adiantoides (Unger) Heer

Pinaceae
Pinus Knowltoni Chaney
Sequoia Langsdorfii (Brongn.) Heer
Glyptostrobus oregonensis R. W. Brown

ANGIOSPERMAE

Typhaceae
Typha Lesquereuxi Cockerell

Salicaceae
Populus Alexanderi Dorf
P. eotremuloides Knowlt.
P. washoensis R. W. Brown
Salix inquirenda Knowlt.

Juglandaceae
Carya egregia (Lesq.) LaMotte

Betulaceae
Alnus carpinoides Lesq.
A. relata (Knowlt.) R. W. Brown
Betula Bendirei Knowlt.
B. Fairii Knowlt.
Ostrya oregoniana Chaney

Fagaceae
Castanea castaneaefolia (Unger) Knowlt.
C. orientalis Chaney
Castanopsis convexa (Lesq.) Brooks
Fagus pacifica Chaney
Quercus Brownii Brooks
Q. consimilis Newb.
Q. idahoensis Knowlt.
Q. (Lithocarpus) klamathensis MacG.
Q. malheurensis H. V. Smith
Q. simulata Knowlt.

Q. Treleasii Berry

Ulmaceae
Ulmus owyhiensis H. V. Smith

Berberidaceae
Mahonia malheurensis Arnold
M. reticulata (MacG.) R. W. Brown
M. simplex (Newb.) Arnold
M. Trainii Arnold

Lauraceae
Sassafras hesperia Berry
Umbellularia oregonensis Chaney

Platanaceae
Platanus aceroides Goepp.
P. dissecta Lesq.
P. regularis Knowlt.

Rosaceae
Amelanchier typica Lesq.
Prunus covea Chaney

Rutaceae
Ptelea enervosa H. V. Smith

Simarubaceae
Ailanthus Lesquereuxi Cockerell

Meliaceae
Cedrela oregoniana (Lesq.) R. W. Brown

Anacardiaceae
Rhus oregonensis H. V. Smith

Aceraceae
Dipteronia insignis (Lesq.) R. W. Brown
Acer Bendirei Lesq.
A. Bolanderi Lesq.
A. negundoides MacG.
A. Osmonti Knowlt.
A. Scottiae MacG.

Sapindaceae
Sapindus oregonianus Knowlt.?

Araliaceae
Oreopanax dissecta (Lesq.) H. V. Smith

Cornaceae
Cornus ovalis Lesq.
Nyssa Knowltoni Berry
N. oregonensis H. V. Smith

Ericaceae
Arbutus idahoensis (Knowlt.) R. W. Brown

Oleaceae
Fraxinus succorensis Arnold

Caprifoliaceae
Symphoricarpos elegans (Lesq.) H. V. Smith

Of the 37 genera, 23 now occur in the West. Some of these, such as *Sequoia* and *Castanopsis*, are found only in the coastal regions, although the majority are widely distributed. Three genera, *Dipteronia, Ginkgo,* and *Glyptostrobus*, are now confined to Asia. *Castanopsis, Lithocarpus,* and *Cedrela* are chiefly Asiatic but have representatives in the Americas.. *Sassafras* is a genus of two species, one of which is native to eastern America, the other to eastern Asia (Formosa). *Carya, Castanea, Fagus, Nyssa, Ostrya, Sassafras,* and *Ulmus* were all widely distributed and quite common in the northwest during the Tertiary but have become extinct there and now grow in eastern America and eastern Asia. Such widely ranging temperate-zone genera as *Acer, Alnus, Amelanchier, Betula, Cornus, Mahonia, Pinus, Populus, Prunus, Salix,* and *Symphoricarpos* are common in such nearby mountainous regions as the Blue Mountains of Oregon and the Boise Mountains of Idaho. Because of the present aridity of the Sucker Creek region, trees are found only along the stream itself and include willows, poplars, alders, and cherries.

A comparison of the fossil and supposedly equivalent living species provides a good method of interpreting the phytogeography of the flora. The majority of such modern species are American and are about equally divided between eastern and western United States.

The following list gives the fossil species which have supposed living equivalents in the western United States:

Fossil species	Related living species
Acer Bendirei	*A. macrophyllum* Pursh
Acer negundoides	*A. Negundo* L.
Alnus carpinoides	*A. sinuata* Rydb.
Betula Bendirei	*B. occidentalis* Hook.
Castanopsis convexa	*C. sempervirens* (Kellogg) Dudley
Cornus ovalis	*C. Nuttallii* Audubon
Mahonia reticulata	*M. Aquifolium* Nutt.
Mahonia Trainii	*M. nervosa* Nutt.
Pinus Knowltoni	*P. attenuata* Lemm.
Populus Alexanderi	*P. trichocarpa* T. & G.
Populus eotremuloides	*P. trichocarpa* T. & G.
Prunus covea	*P. emarginata* Walp.
Quercus Brownii	*Q. chysolepis* Lieb.
Quercus (Lithocarpus) klamathensis	*Lithocarpus densiflora* (H.&A.) Rehd.
Rhus oregonensis	*R. trilobata* Nutt.
Salix inquirenda	*S. lasiandra* Bentham
Sequoia Langsdorfii	*S. sempervirens* Endl.
Symphoricarpos elegans	*S. racemosus* Michx.

Of the above, *Acer Negundo* and *Symphoricarpos* are widely distributed and so are not very significant. Of particular interest is the fact that none of the living equivalents is characteristic of high mountains and some, *Castanopsis, Sequoia,* and *Acer macrophyllum,* usually occur at low elevations. A number of the others are stream border species. The live oak and Mahoniae often occur on fairly dry ridges.

One species, *Umbellularia oregonensis,* should perhaps be added to the above list. It was not included, although reported from Sucker Creek, because I feel that its presence has not been adequately demonstrated. Many paleobotanists would include *Platanus dissecta* with *P. racemosa* Nutt. in the above list. However, I believe that the marignal dentation and lobing relate the fossil species more closely to the eastern *P. occidentalis* L. Ecologically it may have been more like the western species. This species together with *Quercus Brownii, Q. simulata,* and *Castanopsis convexa* are among the most abundant at Sucker Creek.

The following list enumerates the Sucker Creek species which have supposed living equivalents in the eastern United States:

Fossil species	Related living species
Acer Osmonti	*A. saccharinum* L.
Acer negundoides	*A. Negundo* L.
Amelanchier typica	*A. canadensis* (L.) Medic.
Carya egregia	*C. ovata* K. Koch
Castanea castaneaefolia	*C. pumila* Mill.
Fagus pacifica	*F. grandifolia* Ehrhart
Fraxinus succorensis	*F. americana* L.?
Nyssa Knowltoni	*N. aquatica* L.
Nyssa oregonensis	*N. aquatica* L.
Ostrya oregoniana	*O. virginiana* (Mill.) K. Koch
Platanus dissecta	*P. occidentalis* L.
Populus washoensis	*P. grandidentata* Michx.
Ptelea enervosa	*P. mollis* M. A. Curtis var. *cryptoneura* Bartlett

Quercus malheurensis	*Q. alba* L. ?
Quercus Treleasii	*Q. imbricaria* Michx.
Sassafras hesperium	*S. albidum* (Nutt.) Nees
Symphoricarpos elegans	*S. racemosus*
Ulmus owyhiensis	*U. racemosa* Thomas?
Woodwardia deflexipinna	*W. virginica* (L.) Smith

Of the sixteen genera in the above list, seven are not now found in the western United States. They occur in eastern America and eastern Asia and are represented by only a few specimens each in the Sucker Creek flora. The majority of the equivalent living species are important and characteristic members of the mesophytic hardwood forest of the eastern United States. This type of association grows where there is ample rainfall, that is, from 30 to 40 inches per year. Some species such as the *Ostrya* and *Nyssa* grow in wet or swampy places, while the *Populus* and *Sassafras* may grow on rather dry sandy places.

The following smaller list of species have supposed living equivalents in eastern Asia:

Fossil species	Related living species
Acer Bolanderi	*A. Buergerianum* Miq.
Acer Scottiae	*A. pictum* Thunb.
Ailanthus Lesquereuxi	*A. glandulosa* Desf.
Alnus relata	*A. japonica* Sieb. & Zucc.
Betula Fairii	*B. luminifera* Winkler
Castanea orientalis	*C. Henryi* Rehd.
Dipteronia insignis	*D. sinensis* Oliver
Ginkgo adiantoides	*G. biloba* L.
Glyptostrobus oregonensis	*G. heterophylla* Endl.
Mahonia simplex	*M. japonica* Thunb.

Three of these genera, *Dipteroni*, *Ginkgo*, and *Glyptostrobus*, are confined to eastern Asia. The *Ailanthus* is represented by both leaves and samaras. The leaves are those previously called *Apocynum indianum*, the generic reference of which I have previously questioned (13). Further consideration has led me to the belief that the leaves represent *Ailanthus* and the species may therefore be synonymized with *A. Lesquereuxi*, samaras of which Arnold (3) reported from Trout Creek and Sucker Creek.

A few Sucker Creek fossils seem to have their living equivalents in the arid southwestern United States, Mexico, and South America. *Cedrela oregoniana* resembles *C. mexicana* which occurs in Mexico and the West Indies. *Quercus simulata* is quite similar to *Q. hypoleuca* Engelm. although it is also often compared to the Asiatic species *Q. myrsinoefolia* Blume. *Arbutus idahoensis* does not appear to be exactly similar to any living species but is quite close to *A. arizonica* Sarg. from southern Arizona and Mexico and to *A. glandulosa* M.&G. No living species of *Oreopanax* has been noted that is exactly like the fossil one. The genus is one that occurs mostly in Central and South America.

For a few species no satisfactory living equivalent can be given. No closely

similar living equivalent has been noted for *Mahonia malheurensis*. In the comparison of *Platanus aceroides* and *P. regularis* a careful study of all living species was not possible because the available material was not sufficient. From the range in variation exhibited in *P. occidentalis*, however, it appears that both fossil "species" might be referred to that living species. Further comparison of living species with the abundant *Platanus* leaves from Sucker Creek is needed. *Quercus idahoensis* and *Q. consimilis* are hard to match among living types. The first is but poorly illustrated in the literature and so far as I am aware it has not been carefully compared with living species. *Q. consimilis* is in a state of considerable confusion for a discussion of which LaMotte (9) and Brooks (6) should be consulted. Small oak-like leaves are exceedingly common in the western Miocene in general and at Sucker Creek in particular, so it is unfortunate that their relationships are not better known. *Sapindus oregonianus* was reported by Brooks and my collections include the same leaf type. I am inclined to the belief that it is really a *Sapindus* but probably not *S. oregonianus* which some paleobotanists now refer to *Cedrela*. Further study of these leaves is necessary before the living equivalent can be determined.

Two principal ecological associations seem to be included in the flora in addition to the actual stream border species, these may be referred to as the mesophytic lowland association and the more xerophytic upland association. The various species of *Alnus, Betula, Salix,* cottonwood-like *Populus,* and *Platanus* may well have grown along the stream or lake borders. Remains of *Typha* are fairly abundant and indicate a lake or stream border or swampy environment.

The mesophytic lowland association included such typical eastern American hardwoods as *Carya, Castanea, Fagus, Ostrya, Nyssa, Acer* of the *A. saccharinum* type, *Amelanchier* of the *A. canadensis* type; the western species *Sequoia* and *Cornus;* and the Asiatic *Glyptostrobus*.

The more xerophytic plants probably grew on sandy or gravelly banks or low ridges and included such plants as the small-leaved oaks, *Castanopsis, Arbutus, Pinus, Sassafras, Mahonia, Cedrela,* and *Populus* of the *P. grandidentata* type, etc. There is no plant evidence of great topographic diversity at Sucker Creek since conifers are quite rare. This scarcity may, however, be due in part to accident of preservation.

Unlike the earlier Miocene floras from central Oregon, the Sucker Creek flora has only an inconspicuous redwood and redwood border element. Instead, *Platanus* and small-leaved oaks resembling those of the chaparral of California or small Mexican species predominate. In its general aspect the Sucker Creek flora seems to be allied to the Latah of Spokane, Washington, and northern Idaho more closely than to the nearby Weiser, Trout Creek or Thorn Creek floras. The Weiser flora as set forth by Dorf (8) is of late Miocene or Pliocene age and finds its closest affinitty with western forests, especially those of the Coast Ranges of California where the *Lithocarpus-Quercus-Arbutus* community dominates. MacGinitie (11) found that the Trout Creek flora lacked many of the usual eastern American genera common in the western Miocene. He believed the area in which the nearest equivalent living associa-

tion now grows is the Klamath Mountains of southern Oregon and northern California. The principal association there is *Lithocarpus-Arbutus-Pseudotsuga-Chamaecyparis*. The Trout Creek flora also resembles to a rather marked extent the flora of northern Japan and Manchuria. The Latah flora according to Berry (4) "is rather closely paralleled among existing floras by those of such a Middle Atlantic State as Maryland." An appreciable Asiatic element is also included. The Thorn Creek flora (Smith, 14) has an aspect quite unlike that of Sucker Creek. So far as is now known it lacks *Platanus* entirely and small oak-like leaves are not particularly abundant. The numerical dominants are of typical eastern American aspect and are closely related to *Fagus grandifolia* and *Quercus Prinus*. As to number of species there is an almost equal division of those whose nearest living equivalents are in eastern America and those of the northern Rocky Mountains.

It may be postulated that the physical and climatic conditions at Sucker Creek were not unlike those of the low hills of northern California and southern Oregon or the rolling region of southern Michigan. A rainfall of 30 to 40 inches annually with no prolonged summer dry spell would also be indicated.

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A Comparison of Leaf Tissues of Gaylussacia baccata Grown under Different Conditions

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Procedure

In our earlier report (Cain & Potzger, 1933) a comparison was made of plants of *Gaylussacia baccata* grown under usual greenhouse conditions, in a greenhouse room with high evaporation, and in the field. The field studies were from the native upland oak habitat from which the greenhouse plants were transplanted (Cain & Friesner, 1929). The plants from the field condition showed leaves much thicker than those of the greenhouse conditions. It was thought that the field factors which probably had caused the greater thickness of leaves were soil moisture deficiency at intervals during the expansion of the leaves and the greater light intensity, especially with respect to ultra-violet light.

In the present experiments it was not feasible to refit the greenhouse rooms with special glass which would transmit ultra-violet, so temporary wooden-framed shelters were constructed on a small roof on the north side of the science building at Butler University. These two shelters were covered with a common commercial wire-reinforced cloth which was at once water-proof and transmitted a high percentage of ultra-violet light, although with a considerable reduction in total light intensity. The two shelters were open at the sides but were separated by a partition of the same cloth used for the roof. The tubs of plants under one shelter were exposed to the continuous action of a 12-inch revolving electric fan from April 21, previous to the expansion of the buds, to the close of the experiment. To anticipate the results somewhat, it became apparent that the enclosure, through reduction of the intensity of the light or other factors, resulted in leaves that were not greatly thickened in comparison with the previous investigations. Two tubs under each shelter were watered frequently so that the soil was always in good tilth. Two other tubs were watered at less frequent intervals and only when the soil had become so dry that certain small herbs and mosses (which were present in the undisturbed soil when the shrubs were transplanted from the field) showed wilting. In this connection Maximov (1929, p. 370) says, 'In the case of dry cultures, instead of keeping the soil moisture at a constant low level, the soil may from time to time be allowed to dry out until the plant begins to wilt, when water —to the so-called optimum—is again added. . . . As regards structure, the periodically wilted plants were distinguished by marked xeromorphy."

The amount of water supplied the various tubs during the eleven weeks of the experiment is shown in Table 1. The evaporation conditions, as measured by Livingston spherical atmometers, are described in Table 2.

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TABLE 1.—Total amounts of water supplied the different tubs of plants during the experimental period. Figures in liters.

	Fan room				Fanless room			
	Moist soil		Dry soil		Moist soil		Dry soil	
	A		B		C		D	
	1	3	2	4	9	11	10	12
Total water per tub	21	20.5	12	12	17.5	17.5	10	9
Average per tub	20.7		12.0		17.5		9.5	
Ratio: Dry/Moist	0.58				0.51			

TABLE 2.—Evaporation rates under the two shelters for the period, May 28 to August 6, 1933. Figures in cc.

	Fan room	Fanless room
Average total loss (2 atmometers each)	3,197	2,198
Average weekly loss	291	199
Average daily loss	41.5	28.5
Ratio: Fanless/Fan	0.69	

The leaves on which the present studies are based were collected late in June after the leaves were apparently fully expanded. Other collections were made in August, but they have not been studied. It was found in the earlier work, Cain & Potzger (1933), that there were only slight differences in tissue development between June and August—only the sponge parenchyma being significantly thicker. Twenty leaves were taken as a random sample of each condition of growth, cut transversely in half and preserved in formalin-acetic-alcohol. Strips of these leaves were imbedded in paraffin, sectioned, and stained. These sections were uniformly made near the center of the leaf and measurements of the tissues were made at a point on the section roughly 370 microns from the midvein. The necessity for this careful control is discussed elsewhere.

The measurements of leaf area, leaf length and width, stomatal frequency per unit area, and total vein length per unit area were also made on preserved leaves. The leaf area studies were made by means of a polar planimeter from outline tracings of 100 leaves for each condition of growth. The vein length per unit area determinations were made from 80 drawings obtained in the following way: A projection apparatus was used with a 5x ocular and a 16 mm. objective, with tube and Abbey condenser, the upright being adjusted at 35 cm. This gave an image of about 5 3/16 inches. The total length of veins of all sizes in the field of vision was measured by use of a "map measurer," or curvimeter. The apical halves of the leaves were mounted in water and projected onto white paper for the drawing. The stomatal frequencies per unit area also were determined from these projections.

Results

THE GROSS FEATURES OF THE LEAVES

Table 3, concerning leaf area, shows that the largest leaves were produced by the plants grown in moist soil tubs in the room with the fan; the smallest leaves by the plants in the dry soil in the fanless room, at a ratio of 1 to 0.46. The other conditions produced results that are not so striking. If the average

area of the leaves measured from all moist soil plants (200 leaves) is compared with those from dry soil plants the ratio is 1 to 0.67. Similarly, if the average area for leaves from the fan room is compared with that of the fanless room the ratio is 1 to 0.75. In other words, the conditions produced by the fan caused less effect on leaf area than the condition of soil moisture deficiency.

TABLE 3.—Average leaf areas of *Gaylussacia baccata* grown under different conditions.

Condition of growth	Tub no.	No. of leaves	Aver. Area, sq. in. and in (sq. cm.)	Sigma	E_M	C.V.
A. Moist soil,	1	50	.70			
fan room	3	48	.64	.67 sq. in.	±.193	±.013	28.8%
B. Dry soil,	2	50	.54	(4.32 sq. cm.)			
fan room	4	50	.54	.54 sq. in.	±.159	±.011	29.5%
3. Moist soil,	9	50	.75	(3.47 sq. cm.)			
fanless room	11	50	.45	.60 sq. in.	±.240	±.016	40.2%
D. Dry soil,	10	50	.26	(3.84 sq. cm.)			
fanless room	12	50	.35	.31 sq. in. (1.99 sq. cm.)	±.088	±.006	25.9%

Ratio: moist to dry tubs=1:0.67.
Ratio: fan to fanless tubs=1:0.75.
Ratio: moist to dry tubs in fan room=1:0.80.
Ratio: moist to dry in fanless room=1:0.52.

TABLE 4.—The significance of differences of average leaf sizes of *Gaylussacia baccata* grown under different conditions.

Growing conditions compared	Differences between averages	Statistical value of difference
Moist soil: fan room with dry soil: fan room	.13 sq. in.	7.7
Moist soil: fan room with moist soil: fanless room	.07 sq. in.	3.5
Moist soil: fan room with dry soil: fanless room	.36 sq. in.	25.3
Dry soil: fan room with *Moist soil: fanless room*	.08 sq. in.	2.9
Dry soil: fan room with dry soil: fanless room	.23 sq. in.	18.8
Moist soil: fanless room with dry soil: fanless room	.29 sq. in.	16.7

In the conditions italicized in the above table the largest leaves were produced. For example, in the first comparison the leaves averaged 0.13 sq. in. larger in the moist soil than in the dry soil of the fan room.

Table 4, giving the statistical value of the differences between the growing conditions, shows that the smallest value, 2.9, has only about 1 out of 20 chances of being due to the chance of the sample. In the next larger value the probability is about 54 to 1 that the difference is not due to chance but to the difference in the growing conditions which are compared. In the rest of the comparisons, the value is so great that the differences are undoubtedly due to the growing conditions. Although the plants were all collected from the same field clump, the plants from tubs 9 and 11 in the moist soil of the fanless room were very different with respect to leaf area for some unknown reason. No

known difference in treatment would seem to be the cause. All comparisons with respect to leaf area would have had even greater significance were it not for this set which has a coefficient of variation of 40.2 per cent.

TABLE 5.—Average leaf lengths and widths of *Gaylussacia baccata* grown under different conditions. Measurements in cm.

Condition of growth	Tub	No. of Leaves	Average leaf length	Sigma	E_M	C.V.
A. Moist soil, fan room	1	50	3.8	±.56	±.038	15.0%
	3	50	3.7 } 3.75 cm.			
B. Dry soil, fan room	2	50	3.5	±.57	±.038	16.2%
	4	50	3.4 } 3.45 cm.			
C. Moist soil, fanless room	9	50	3.9	±.67	±.049	19.3%
	11	50	3.1 } 3.48 cm.			
D. Dry soil, fanless room	10	50	2.3	±.40	±.034	16.0%
	12	50	2.7 } 2.52 cm.			
			Average leaf width			
A. Moist soil, fan room	1	50	1.7	±.64	±.043	39.3%
	3	50	1.6 } 1.64 cm			
B. Dry soil, fan room	2	50	1.4	±.20	±.013	13.8%
	4	50	1.4 } 1.43 cm			
C. Moist soil, fanless room	9	50	1.7	±.31	±.021	20.5%
	11	50	1.3 } 1.50 cm.			
D. Dry soil, fanless room	10	50	1.0	±.16	±.011	14.2%
	12	50	1.2 } 1.12 cm.			

TABLE 6.—The significance of differences of average leaf lengths and widths of *Gaylussacia baccata* grown under different conditions.

Growing conditions compared	Differences between averages		Statistical value of difference	
	Length	Width	Length	Width
Moist soil: fan room with Dry soil: fan room	.30 cm.	.21 cm.	5.6	4.9
Moist soil: fan room with Moist soil: fanless room	.27 cm.	.14 cm.	4.4	3.0
Moist soil: fan room with Dry soil: fanless room	1.32 cm.	.52 cm.	23.6	11.5
Dry soil: fan room with *Moist soil: fanless room*	.03 cm.	.07 cm.	.5	2.8
Dry soil: fan room with Dry soil: fanless room	.93 cm.	.31 cm.	18.1	17.2
Moist soil: fanless room with Dry soil: fanless room	.96 cm.	.38 cm.	16.1	15.9

Tables 5 and 6, for average leaf lengths and widths, reveal the same general relationships as Tables 3 and 4. However, the coefficient of variation is smaller in all cases except for condition A. The only comparison where no difference of statistical significance is revealed is that of leaf lengths when condition B is compared with condition C.

Tables 7 and 8, for total vein lengths per unit, reveal results directly comparable to those already described (Tables 4-6). The magnitude of the measurements are reversed, for the smaller leaves have greater vein length per

unit area. The leaves from plants of dry soil have greater vein length per unit area than the leaves of plants from moist soil. In the dry soil plants those of the fanless room have greater vein lengths than those of the fan room. In the moist soil plants no distinction appears with respect to the influence of the fan.

TABLE 7.—Average vein lengths per unit area of leaves of *Gaylussacia baccata* grown under different conditions. The 80 measurements made by a curvimeter in inches from drawings of projected images of leaves.

Condition of growth	Tub no.	No. of leaves	Average vein length in inches & cm.	Sigma	E_M	C.V.
A. Moist soil, fan room	1	10	38.9 } 39.85 in.	±4.24	±.642	10.6%
	3	10	40.7 } (101.2 cm.)			
B. Dry soil, fan room	2	10	42.8 } 44.05 in.	±4.35	±.656	9.9%
	4	10	45.3 } (111.9 cm.)			
C. Moist soil, fanless room	9	10	36.1 } 39.33 in.	±6.52	±.985	16.5%
	11	10	42.5 } (99.9 cm.)			
D. Dry soil, fanless room	10	10	60.6 } 56.49 in.	±8.11	±1.22	14.3%
	12	10	52.4 } (143.5 cm.)			

TABLE 8.—The significance of differences of average vein lengths of *Gaylussacia baccata* grown under different conditions.

Growing conditions compared	Differences between averages	Statistical value of difference
Moist soil: fan room with *Dry soil: fan room*	4.20 in.	4.5
Moist soil: fan room with Moist soil: fanless room	.52 in.	.4
Moist soil: fan room with *Dry soil: fanless room*	16.64 in.	12.0
Dry soil: fan room with Moist soil: fanless room	4.72 in.	4.0
Dry soil: fan room with *Dry soil: fanless room*	12.44 in.	9.0
Moist soil: fanless room with *Dry soil: fanless room*	17.16 in.	10.9

In the above table the growing condition italicized has the greater unit area vein length in any comparison.

THE PROTECTIVE TISSUES OF THE LEAVES

A. *The Stomata.*—In Tables 9 and 10, with reference to number of stomata per unit area, the results are directly comparable to those of Tables 7 and 8, reduction in leaf size results in an increase in total vein length and stomatal number per unit area. This increase in stomatal frequency is especially striking when dry soil plants are compared with moist soil plants in either room. When moist soil plants are compared with moist soil plants the conditions of the fanless room produce greater stomatal density, and this is especially true when dry soil plants are compared.

B. *The Epidermis.*—Under all conditions of growth, the upper epidermis

is thicker than the lower epidermis. The greatest difference is in the dry soil plants of the fanless room, while the least difference is in the dry soil plants of the fan room, Table 11.

With respect to conditions of growth, Tables 11-13, it is seen that the upper epidermis is significantly smaller in the dry soil in the fan room. Also, in comparing B with C and B with D, the difference is statistically significant. In the latter both are dry soil plants, those of the fan room showing the smallest cells. For the lower epidermis, only the dry and moist soil plants of the fan room (A with B) show a difference value of 3. In all cases the coefficient of variation is much less for epidermal thickness than for cuticle, ranging from 11.5 to 20.4 per cent. The upper epidermis shows the greatest plasticity, averaging 14.6 microns thick in the dry soil and 18.0 microns thick in the moist soil of the fan room. The lower epidermis ranges only between 14.0 and 15.7 microns, and for the same growing conditions. The greater plasticity then is revealed in the room with the higher evaporation rate: that is, the epidermal differences, of the upper and lower epidermis of moist and dry soil plants, are more accentuated in the fan room.

TABLE 9.—Average number of stomata per unit area, upper and lower epidermis, of *Gaylussacia baccata* grown under different conditions.

	Fan room		Fanless room	
Upper epidermis	Moist soil	Dry soil	Moist soil	Dry soil
	A	B	C	D
Average	10.3	14.4	10.0	21.2
Standard deviation	± 2.80	± 4.57	± 3.75	± 7.0
Probable error	± .44	± .68	± .58	± 1.08
Coefficient of variation	27 %	31 %	37 %	33 %
Lower epidermis				
Average	48.5	59.1	63.0	89.9
Standard deviation	± 9.72	± 13.08	± 18.0	± 24.25
Standard deviation	± 9.72	± 13.08	± 18.0	± 24.25
Probable error	± 1.46	± 2.02	± 2.72	± 3.71
Coefficient of variation	20 %	22 %	28 %	27 %

TABLE 10.—The significance of differences of average number of stomata per unit area of leaves of *Gaylussacia baccata* grown under different conditions.

Condition of growth compared	Upper epidermis		Lower epidermis	
	Difference	Value	Difference	Value
Moist soil: fan room with *Dry soil: fan room*	4.1	5.0	10.6	4.2
Moist soil: fan room with *Moist soil: fanless room*	.3	.4	14.5	4.6
Moist soil: fan room with *Dry soil: fanless room*	10.9	9.3	41.4	10.4
Dry soil: fan room with Moist soil: fanless room	4.4	4.9	3.9	1.0
Dry soil: fan room with *Dry soil: fanless room*	6.8	5.3	30.8	7.3
Moist soil: fanless room with *Dry soil: fanless room*	11.2	9.1	26.9	5.8

In the conditions which are compared above, the greater number of stomata are

produced by that condition italicized, with two exceptions, that of the second comparison for the upper epidermis, and here the difference is insignificant, and that of the lower epidermis in the fourth comparison, where, also, there is no significant difference.

C. *The Cuticle.*—Under all conditions of growth the upper cuticle on the blades averages thicker than the lower cuticle. The least difference is in leaves from the moist soil tubs of the fan room. The greatest difference is in the moist soil plants of the fanless room, although the dry soil plants of both rooms show almost equal differences with the latter, Table 11. In the midvein

TABLE 11.—Average blade, tissue, and cuticle thicknesses in microns of leaves of *Gaylussacia baccata* grown under different conditions.

Condition of growth	Tub no.	Upper cuticle	Upper epiderm.	Palisade	Sponge parenchyma	Lower epiderm.	Lower cuticle	Total blade
A. Moist soil,	1	1.52	17.00	21.72	39.66	14.54	1.12	95.56
fan room	3	1.80	19.04	24.48	37.74	16.83	1.55	101.44
Average		1.66	18.02	23.10	38.70	15.68	1.33	98.50
Sigma		±.42	±2.98	±5.18	±7.23	±2.76	±.52	±11.34
Probable error		±.068	±.485	±.843	±1.119	±.427	±.082	±1.847
Coef. variat.		25.3%	16.5%	22.4%	18.6%	17.6%	39.1%	11.5%
B. Dry soil,	2	2.16	14.45	22.78	33.66	13.28	1.54	87.87
fan room	4	1.88	14.79	18.87	37.06	14.79	1.15	88.54
Average		2.02	14.62	20.82	35.36	14.03	1.34	88.20
Sigma		±.52	±2.61	±4.37	±6.08	±2.45	±.40	±9.26
Probable error		±.073	±.405	±.674	±.917	±.370	±.061	±1.429
Coef. Variat.		25.7%	17.8%	21.0%	17.2%	17.4%	30.0%	10.5%
C. Moist soil,	9	2.05	17.41	25.33	44.20	15.30	1.29	105.58
fanless room	11	1.47	17.51	25.16	35.02	15.47	1.22	95.85
Average		1.76	17.46	25.24	39.61	15.38	1.25	100.71
Sigma		±.64	±3.56	±5.15	±11.55	±1.78	±.41	±12.78
Probable error		±.099	±.551	±.782	±1.740	±.270	±.062	±1.976
Coef. variat.		36.3%	20.4%	20.4%	29.1%	11.5%	33.0%	12.7%
D. Dry soil,	10	2.31	18.02	22.78	36.89	14.11	1.55	95.66
fanless room	12	1.72	17.03	22.78	34.23	14.88	1.37	92.01
Average		2.01	17.52	22.78	35.56	14.49	1.46	93.83
Sigma		±.78	±2.13	±7.13	±6.99	±2.05	±.45	±11.35
Probable error		±.121	±.330	±1.098	±1.052	±.310	±.069	±1.754
Coef. variat.		38.8%	12.1%	31.3%	19.6%	14.1%	30.8%	12.1%

These averages are based on 20 leaves for each condition of growth.

region, Table 16, the condition is reversed, for the lower cuticle is found to be about 2 to 3 times thicker than the upper cuticle. With respect to the two regions of the leaves, Table 18, it is seen that the upper cuticle averages thicker in the midvein region for the moist soil plants and slightly thinner in this region for the dry soil plants. As to lower cuticle, it is much thicker (3.2 to 4.5 times) in the midvein region than it is on the blade, again being somewhat more in the moist soil plants, and especially in the fanless room.

With respect to the conditions of growth, it is seen that, Tables 11-13, the cuticle on both surfaces of the blades tends to average thicker in dry soil than in moist soil. However, the difference is significant (value of 3 or more) for

the upper cuticle only in the fan room. It would seem that for the dry soil plants under higher evaporation the cuticular material tends to concentrate more on the upper surface. For the lower cuticle the difference is never significant. The great variability in cuticle thickness from leaf to leaf on the same plant and between plants grown under identical conditions is revealed by the averages for the two tubs of each set and by the coefficient of variation for the entire sample, which ranges from 25 to 39 per cent. In the midvein region the upper cuticle is significantly thicker in the moist soil plants than for the dry soil plants of both rooms, Table 17, and for the lower cuticle in the fanless room. The difference with the greatest statistical value (7.8) is for the fourth comparison of upper cuticle, the moist soil plants of the fanless room with the dry soil plants of the fan room. It would seem that adequate moisture and lower evaporation caused the greatest relative cuticle deposition on the upper surface. This is the reverse of the result for the blades.

TABLE 12.—The significance of differences of average tissue and cuticle thickness of *Gaylussacia baccata* leaves grown under different conditions. Differences are in microns: D. V = statistical value.

		Growing conditions compared					
Tissue		A with B	A with C	A with D	B with C	B with D	C with D
Upper cuticle	D	.36	.10	.35	.26	.01	.25
	V	3.6	.8	2.4	2.1	.07	1.6
Upper epidermis	D	3.40	.56	.50	2.84	2.90	.06
	V	4.8	.7	.8	4.1	4.9	.08
Palisade	D	2.82	2.14	.32	4.42	1.96	2.46
	V	2.6	1.8	.2	3.7	1.5	1.7
Sponge parenchyma	D	3.34	.91	3.14	4.25	.20	4.05
	V	2.3	.4	2.0	2.1	.15	2.0
Lower epidermis	D	1.65	.30	1.19	1.35	.46	.89
	V	3.0	.6	2.3	2.9	.9	2.1
Lower cuticle	D	.01	.08	.13	.09	.12	.21
	V	.1	.8	1.2	1.0	1.3	2.3
Total blade	D	10.30	2.21	4.67	12.51	5.63	6.88
	V	4.4	.9	1.8	5.1	2.5	2.6

Each figure is based on the average of 20 leaves.

TABLE 13.—Ratios between tissue and cuticle thicknesses of leaves of *Gaylussacia baccata* grown under different conditions.

Tissue	Fan room dry:moist	Fanless room dry:moist	Moist plants fan:fanless	Dry plants fan:fanless
Upper cuticle	1: .82	1: .87	1:1.06	1:1.0
Upper epidermis	1:1.22	1:1.0	1: .97	1:1.11
Palisade	1:1.11	1:1.10	1:1.09	1:1.09
Sponge parenchyma	1:1.10	1:1.11	1:1.02	1:1
Lower epidermis	1:1.11	1:1.06	1: .98	1:1.03
Lower cuticle	1: .99	1: .83	1: .94	1:1.09
Total blade	1:1.11	1:1.07	1:1.02	1:1.07
	A	B	C	D
Palisade/sponge ratios	.59	.59	.63	.64

The Photosynthetic Tissues

The depth of the palisade region shows an orderly arrangement with respect to soil moisture and evaporation, the relationship being direct with soil moisture and inverse to the evaporation: averaging smallest, 20.8 microns, in the dry soil of the fan room (B); 22.8 microns, in the dry soil of the fanless room (D); 23.1 microns, in the moist soil of the fan room (A); and thickest, 25.3 microns, in the moist soil of the fanless room (C), Table 11. However, only at the extremes (B compared with C) is the difference statistically significant, with a value of 3.7, Table 12. The coefficient of variation is large, ranging from 20.4 to 31.3 per cent. This is due in part to the difficulty of determining in some cases the lower limits of the palisade region when the row of palisade cells is incomplete.

The sponge parenchyma shows the same sequence of average thickness as the palisade, forming an increasing series with conditions B, D, A, and C. These differences, however, are never of statistical significance but range from a value of 2 to 2.3 when moist and dry soil plants are compared. It would seem, Tables 11-13, that the palisade is somewhat more plastic than the sponge.

The palisade sponge ratio, Table 13, is the same (0.59) for both moist and dry soil plants of the fan room, while the palisade is relatively thicker in the fanless room with ratios of 0.63 for moist and 0.64 for dry soil plants.

Table 14.—Average widths of palisade cells of *Gaylussacia baccata* grown under different conditions. Measurements in microns.

	Fan room		Fanless room	
	Moist soil	Dry soil	Moist soil	Dry soil
	A*	B	C	D
Width (200 measurements, 10 @ on 20 leaves)	10.3	9.86	10.81	9.42
Standard deviation	±1.63	±1.36	±1.53	±1.20
Probable error	± .082	±.065	±.073	±.057
Coefficient of variation	15.8%	13.8%	14.1%	12.7%

* Condition A is based on only 190 measurements.

Table 15.—Significance of differences of palisade cell thickness (width) of *Gaylussacia baccata* grown under different conditions. Differences in microns.

Condition of growth	Differences between averages	Statistical value of differences
Moist soil: fan room with Dry soil: fan room	.44	4.2
Moist soil: fan room with *Moist soil: fanless room*	.51	4.6
Moist soil: fan room with Dry soil: fanless room	.87	8.7
Dry soil: fan room with *Moist soil: fanless room*	.95	9.7
Dry soil: fan room with Dry soil: fanless room	.43	5.0
Moist soil: fanless room with Dry soil: fanless room	1.38	15.0

TABLE 16.—Average thickness of leaves at the midvein and of the upper and lower cuticle at the midvein; *Gaylussacia baccata* grown under different conditions. Measurements in microns.

	Fan room		Fanless room	
	A* Moist soil	B Dry soil	C Moist soil	D Dry soil
Midvein (20 leaves each)				
Average thickness, leaf	300.2	262.9	288.2	267.2
Standard deviation	±26.13	±33.56	±40.31	±23.97
Probable error	±4.05	±5.06	±6.07	±3.61
Coefficient of variation	8.7%	12.7%	14.0%	8.9%
Upper cuticle (20 leaves)				
Average thickness	2.4	1.8	3.0	2.08
Standard deviation	±.69	±.64	±.80	±.97
Probable error	±.11	±.09	±.12	±.15
Coefficient of variation	28.7%	35.5%	26.8%	46.6%
Lower cuticle (20 leaves)				
Average thickness	5.5	5.35	5.7	4.7
Standard deviation	±1.30	±1.13	±1.46	±.93
Probable error	±.20	±.17	±.22	±.14
Coefficient of variation	23.6%	21.1%	25.6%	19.8%

* For condition A only 19 leaves were available.

TABLE 17.—Significance of differences of average midvein and cuticle thickness in midvein region of *Gaylussacia baccata* grown under different conditions. Difference in microns.

Condition of growth	Midvein		Cuticle: Upper		Cuticle: Lower	
	D	V	D	V	D	V
Moist soil: fan room with Dry soil: fan room	37.3	5.7	.60	4.2	.20	.7
Moist soil: fan room with Moist soil: fanless room	12.0	1.6	.60	3.7*	.15	.5*
Moist soil: fan room with Dry soil: fanless room	33.0	6.1	.32	1.7	.85	3.5
Dry soil: fan room with *Moist soil: fanless room*	35.2	4.5	1.20	7.8	.35	1.2
Dry soil: fan room with *Dry soil: fanless room*	4.3	.7	.28	1.6	.65	2.9*
Moist soil: fanless room with Dry soil: fanless room	21.0	3.0	.92	4.8	1.00	3.8

D=difference in thickness in microns. V=Statistical value. In each of the above comparisons the condition underlined shows the greatest thickness except in cuticle development marked (*).

TABLE 18.—Comparison of leaf thickness at midvein and on the blade, and of upper and lower cuticle thickness in the two regions.

	Fan room		Fanless room	
	Moist soil	Dry soil	Moist soil	Dry soil
	A	B	C	D
Total leaf thickness Midvein/blade	3.0	3.0	2.8	2.8
Upper cuticle thickness Midvein/blade	1.5	.9	1.5	.9
Lower cuticle thickness Midvein/blade	4.2	4.1	4.5	3.2

If the width of the palisade cells is considered, Tables 14-15, it is seen that they are smaller in dry soil than in moist soil plants and that the difference is greatest in the fanless room with a value of 15. All comparisons result in a value in excess of 3.

Discussion of Stomatal Frequency

Relation of stomatal frequency to height of insertion of leaf.—Zalenski (1902) noted the presence of a denser network of veins in the upper leaves of a plant. He determined this to be due to the smaller size of the cells occupying the space between veins and not to a more elaborate branching of the veins. In accordance with this general change he also found that the number of stomata per unit area of surface increased with the height of the leaf above the soil. Maximov (1929, p. 332) says the result of Zalenski's measurements and observations is to establish the general rule that the anatomical structure of the individual leaves of one and the same shoot is, so to speak, a function of their distance from the root system. This rule, he says, may justly be called "Zalenski's Law." However, similar conclusions by Sorauer (1878) appeared several years earlier. Zalenski noticed very early in his work that the changes in upper leaves of a shoot, as compared with lower leaves, is parallel with conditions in plants of dry habitats as compared with plants of moister habitats; therefore one can conclude that upper leaves are more xeromorphic than lower leaves of the same shoot. Yapp (1912) was the first to obtain data fully in accord with those of Zalenski. Subsequently Zalenski's results were further confirmed by Heuser (1915) and Rippel (1919). Salisbury (1928), in an extensive paper, showed that stomatal frequency for herbs, shrubs and trees alike increased with height above the ground at which the leaf is borne. He also observed that frequencies tended to be higher for trees and shrubs than for herbs. Reed and Hirano (1931), studying citrus leaves, found that the smaller leaves near the apex of the shoot had the greatest, and the larger leaves, one-third of the distance from the base to the apex, had the smallest density of stomata.

Relation of stomatal frequency to dryness of habitat: and other factors.—As mentioned above, Zalenski observed that leaves of higher insertion on the shoot showed the same changes, described as greater xeromorphy, that plants of the same species showed in drier habitats. Bruner and Weaver (1924), studying cereals grown in habitats of different xerophytism, found that the number of stomata increased and leaf area decreased with increasing xerophytism, but both wet and dry weight increased. They record an inverse relationship between size of leaf and number of stomata per unit area. Their results compared favorably with those of Kiesselbach and Keim (1921) on corn grown under conditions differing as to xerophytism. Bahgat (1923), quoted by Hirano (1931), showed that for citrus species the density of stomata on the leaves of a given species or variety was greatest in hot arid regions and least in cool moist regions, and also that shading the leaves reduced the density of stomata and increased their size. Maximov (1929, p. 370) showed that periodically wilted plants were distinguished by marked xeromorphy showing an increase of stomata per unit area of 35 per cent over

the continually moist series. Clements and Long (1935) using phytometers observe some interesting effects of soil water content (based on per cent of holard) and light intensity on the morphology of *Helianthus*. The major correlation in number of stomata (for all holards used in the series) is with light intensity: for the lower epidermis 100 per cent light gave 291 stomata with 99 stomata in 11 per cent light; for the upper epidermis 262 and 120 stomata, respectively. A decrease in soil moisture from 35 to 14 per cent holard gave a change in stomatal numbers (for 100 per cent light) from 315 to 248 for the lower epidermis and 288 to 240 for the upper. However, the relationship was reversed for the series involving 44, 27, 19, and 11 per cent light wherein the drier soils developed plants with a higher stomatal frequency. The authors make the statement, p. 655, that "while the numbers generally follow the relative expansion of the leaf . . . it is clear that the number of stomatal initials varies under the several conditions . . . and to a considerable extent independent of the degree of expansion." Haberlandt (1924, p. 439), after examining the extensive literature, concludes that a far-reaching parallel between the quantity of stomata and the moisture conditions is not to be expected, merely in general remains the principle that with increasing dryness of the habitat the number of stomata increases. In some recent studies where plants were grown under artificial wind but with other factors relatively unchanged Martin and Clements (1935) show that leaf area, stem height and diameter, dry weight, and total transpiration decreased with increasing wind velocity. Microscopic sections of the leaves of plants grown under different wind velocities failed to show any qualitative differences in mesophyll, due evidently to compensation by change of size. They conclude that wind is to be regarded as a factor, though not the paramount one, in the dwarfing characteristics of plants of exposed places. Hirano (1931) observed that rain during the spring months, while young citrus leaves are developing, showed a stronger correlation with the number of stomata than the amount of annual rainfall; although it was impossible to disregard other factors, such as light, heat, and atmospheric humidity. Reed and Hirano (1931) referring to the differences in leaf structure correlated with height of insertion, thought this may be due to the effect of light, the basal leaves being more shaded than apical leaves. Their Table 6 showed the following averages for leaves of *Citrus limonia*: 10 sun leaves, 636 stomata per mm.^{2}, 10 shade leaves, 322 stomata per mm.^{2} Many authors have observed the effect of shading on the reduction of stomatal density and increase of the surface area of epidermal cells. There is no need to go into the extensive literature on sun and shade leaves.

Salisbury (1928), considering the frequency of stomata on different parts of a leaf, emphasized the parallel with increase in suction force and osmotic pressure. He pointed out that Molz (1926) had shown differences in osmotic pressure in various parts of a leaf and in leaves inserted at different heights. Salisbury concluded, however, that the general relation between stomatal frequency and osmotic pressure is not more than a parallel response to differences in the humidity of the environment, as plants of dry exposed situations tend to have high stomatal frequencies and high osmotic pressures. There-

fore, stomatal frequences cannot be regarded as a means of adaptational adjustment with respect to transpiration. With respect to osmotic relationships and structure, see also Dixon and Atkins (1910, 1912), Iljin and Soboleva (1917), Lutman (1919), and Salisbury (1932).

The widely recognized sun and shade differences failed to appear and no significant correlation in stomatal frequency corresponding to differences in illumination was observed for several species when grown under conditions of similar humidity, according to Salisbury (1928). However, comparison of plants grown in moist and dry air indicate that low humidity is associated with high stomatal frequencies.

Finally, Salisbury (1932), emphasizing the mutual interaction between climate, soil, and organism, and that the complexity precludes their direct estimation from determinable data, gave evidence that stomatal frequency is dependent on water relations. Therefore, with due precautions, stomatal frequency can be utilized as a phytometric index of the resultant combination of both internal and external factors: exposure, atmospheric humidity, water content of the soil, water-supplying power of the soil, and various unidentified internal factors.

Relation of cell size to stomatal frequency.—Early morphological work by Sachs (1893), later confirmed by Sierp (1913), seemed to establish that a fairly constant cell size occurred in each species. However, numerous ecological and physiological researches have shown that variations in nutrition and various habitat factors, as light and water balance, produce decided changes in cell size. Kisser (1927) found such variation in the size of epidermal cells and their derivatives, as guard cells, hairs, and the number of stomata per unit area, that he used stomatal data as a measure of the plant's transpiration when grown under different nutrient conditions. Salisbury (1928) using the concept of "stomatal index":

$$\frac{S}{E + S} \times 100.$$

where S equals the number of stomata per unit area and E equals the number of epidermal cells per unit area, showed in general that the stomatal frequencies were a function of cell size and not of the total number of stomata formed. In other words the proportion of stomata formed in the epidermis is no greater for sun leaves than for shade leaves, in dry soil as compared with wet soil, and of small leaves as compared with large leaves of the same species.

Relation of cell size to habitat factors and ontogeny of leaves: influence on stomatal frequency and stomatal index.—Maximov (1929, p. 346) suggested that as the epidermis is the first tissue to be exposed to the atmosphere as the bud expands and to suffer loss of water by cuticular transpiration it is probably the first leaf tissue to have the size of its cells limited. If this is the case, the epidermis, particularly in a dry atmosphere, may play an active part in determining the final structure of the leaf. Reed and Hirano (1931), studying citrus leaves, found that the production of stomata ceased when young leaves were about one-fourth their final size, so that the density of stomata decreased as the area of the leaf increased, after the early stages of growth had passed. Obviously comparisons should be based on fully expanded leaves. Also, any

factors influencing cell size and hastening maturity would of necessity influence stomatal frequency. The general relationship is one of a higher stomatal density per unit area in smaller leaves of a given species. Mounts (1932) has made studies on leaves of *Vitis* and *Catalpa* and found the developmental period to be long enough to avoid adjustment to any temperate factor but would allow modifications with respect to average light and moisture. Attention was called to the fact that "when leaves emerge from the bud the light is many times brighter for all interior leaves than at the conclusion of their development. There must, therefore, be a gradual adjustment throughout their plastic phase to average conditions that are to surround the adult leaf during its functional period." Avery (1933), studying tobacco leaves, pointed out that although the epidermis is the first leaf tissue to stop cell division it is in this tissue that cell enlargement continues longest. His work agrees with that of Miss Mounts with respect to the rôle of the expanding epidermis in the production of intercellular spaces in the mesophyll. Considering the mechanical effect of epidermal cell enlargement it is apparent that not only stomatal frequency is influenced by the mature size of the epidermal cells but also that the general compactness of the mesophyll is correlated with the conditions causing smaller epidermal cells.

One final point as to stomatal frequencies should be mentioned. Lippmaa (1929), in speaking of the large number of stomata per unit area of the species characteristic of the heath (in contrast with species of the woodland, etc.), made the point that the exceptionally high numbers shown by most dwarf shrub heath plants is to be referred back, in part at least, to a similar reason during their phylogenetic development.

Discussion of Palisade Parenchyma

Factors influencing original differentiation and orientation.—Eberdt (1888) believed that most plants are from the first disposed toward at least one layer of palisade parenchyma but that the elongation of its cells and increase of its layers are brought about through the combined action of assimilation and transpiration and that light is not the most important influent. Haberlandt (1881) already had stated that light does not influence the structure of this tissue but only its disposition. He held that the reason palisade is developed is because the products of assimilation ought to be carried away from the assimilation cells by the shortest possible road, and the form of cell best fitted for this rapid translocation is the elongated form. Haberlandt (1924, p. 272), however, made the general statement that the intensity of illumination has determinative influence on the topographic organization of the assimilative tissues. In most cases the light side of the leaf is identical with the morphological upper side, but through the rotation of the petiole or leaf base the morphological underside becomes the light side (Allium, grasses, etc.). There are exceptions, however, and palisade is developed on the shade side of the leaf (in *Corylus avellana, Galium purpureum,* etc.) which shows that the palisade cell form is not always bound up with the highest light intensity. He notes a more or less large plasticity of assimilation tissue which occurs in this

way: bright light yields a direct influence on assimilation tissue through a more energetic assimilation, resulting in a richer development of the assimilation tissue and increased capacity for efficient utilization of the bright light. The single palisade cell becomes longer and the number of cells sometimes is increased. Imamura (1931) by alternating the orientation of developing leaves of *Iris japonica* produced a reversal of the palisade and sponge tissues, showing that the palisade for that species at least is not fixed with respect to the adaxial surface.

Relation of palisade to ontogeny of the leaf.—Avery (1933), working with tobacco leaves, found that the palisade maintains cell division longer than the other tissues of the leaf. The palisade cells begin to acquire their characteristic shape when the leaf is only $^1/_{75}$ to $^1/_{60}$ final size, although they continue to divide for a while thereafter. Intercellular spaces do not develop markedly until the leaf is $^1/_4$ to $^1/_3$ of its final size.

To the authors it would seem that, since the intercellular spaces are schizogynous and their greater volume depends on the continued elongation or expansion of the epidermal cells, factors influencing epidermal cell size would influence the compactness of the mesophyll. Hence, in the case of tobacco, environmental conditions from the time the leaf was $^1/_4$ grown until growth stopped would be effective on the general structure of the leaf. On the other hand, factors influencing shape of individual palisade cells might make their imprint while the leaf was exceedingly small, since shape differentiation begins to appear while the leaf is yet only $^1/_{75}$ grown.

Influence of environmental factors on palisade development.—Stahl (1883) related palisade to light. Dufour (1887) and Pick (1882) thought that the elongated nature of the palisade cell was ancestral, but that for strong development light is necessary. Clements (1905) considered light the principal factor in the development of deep palisade. Pfeiffer (1928), working in greenhouses equipped with glass to transmit light of different qualities, found that in soy bean, in the visible spectrum house, the absence of ultra-violet light resulted in a reduction of the inner palisade layer.

About 50 years ago the general differences between sun and shade leaves were first noted and analyzed. Nordhausen (1903, 1912), who noticed for beech a thicker palisade in sun leaves than in shade leaves, and in apical leaves as opposed to basal shoots, believed that sun and shade characters are predetermined in the bud by former vegetative conditions. Buds formed under shade conditions, if exposed to light in the following season, develop leaves with a shade structure, and conversely, buds formed in strong light will develop sun leaves in the shade. The effect may take more than one season to "wear off." Bergen (1904) noted for *Pistacia* that the palisade is double in the sun and single in the shade leaves, occasionally with a lower palisade in the sun. Skene (1924, p. 153) noted for maple two layers of palisade in sun leaves and one layer in shade leoves. The ratio of thickness of palisade to sponge parenchyma is in the sun leaf 3.9 to 1 and in the shade leaf 1.1 to 1. The total volume of the intercellular spaces is greater in the shade leaves by about 50 per cent. He says, p. 154, "The thin palisade of the shade leaf may be supposed to absorb

efficiently light of low intensity. The sun leaf, with deep palisade, may be regarded as absorbing more efficiently light of higher intensities; the increased energy supply thus available is paralleled by an increased supply of CO_2 through the greater number of stomata per unit area." Büsgen and Münch (1929, p. 224), comparing sun leaves on the surface of the crown of beech, oak, and hazel, with shade leaves from the interior of the crowns, found the latter to be developed as a single layer of cells, rather than as many layers, full of gaps and differing little from the sponge parenchyma. Many workers have found not only an increase in depth of the palisade tissue with increased light but have found that the tissue is proportionately thicker when compared with the whole leaf or with the sponge. Halma (1929) is one of the few who have reported negative results in this respect. Of citrus leaves he found no differences in palisade/leaf thickness ratio from the north and the south sides of trees, and from the top and the bottom leaves of the trees. Moreover, he found values to remain nearly constant for each species or variety regardless of the age of the tree and its geographical distribution. Yapp (1912), studying *Spiraea Ulmaria,* also found the ratio of the total depth of the palisade to that of the sponge mesophyll to be remarkably constant, but that the length and breadth ratio of individual cells showed considerably greater variation. The palisade cells of shade plants tend to be relatively shorter and broader. Furthermore, in an individual leaf those palisade cells which are most remote from the larger veins are relatively longer and narrower than those located near veins.

Vesque and Viet (1881) concluded from their experiments that light and dry air (accelerating transpiration) resulted in a greater development of palisade. Bonnier (1895) added temperature to these two factors. Cooper (1922) found for the broad-sclerophyll vegetation of California increased development of palisade tissue and a decrease of sponge coincident with increase of light and decrease of moisture. Eberdt (1888) thought that increase in palisade development is caused by assimilation and transpiration working together, and that light in itself is never the cause that calls forth palisade parenchyma. Wagner (1892) reported that alpine plants exposed to decreased transpiration did not show a reduction in palisade, and concluded that not transpiration but assimilation was more effective in producing that tissue.

Rippel (1919), working with dry soil and moist cultures of *Sinapis alba,* noted that the fourth leaf in moist cultures had a palisade of 110 to 120 microns while the eighth leaf was 150 microns. The widths were respectively 32 to 40 microns and 12 to 16 microns. A comparison of corresponding dry series shows that the reduction in width of palisade takes place more intensively and earlier than in the moist series leaves. The fourth leaf of a dry soil plant gave palisade dimensions of 200 microns by 16 to 20 microns. Computing the surface of palisade cells of moist and dry grown leaves he found that the dry grown palisade presents twice the surface. The chloroplasts are correspondingly increased. This is borne out by color and the greater photosynthetic activity of xeromorphic leaves, as observed by several workers. Clements and Long (1935) found that a decrease in soil moisture resulted in thinner leaf except for series grown under the lowest light intensity. Reduction of holard resulted in reduction of the palisade from 2 rows to 1½ and 1 row with

decreasing light intensity. Kearney (1900) considered excessive transpiration accountable for both increased palisade and succulency.

Starr (1912), comparing the same species grown on sand dunes and in more mesophytic situations, found a general tendency for the mesophyll to be composed to a greater extent of palisade in the plants grown in the more xerophytic habitat. Lippmaa (1929), studying the same species grown in heath and in woodland habitat, found the palisade/sponge ratio always higher in the heath. For example, *Vaccinium myrtillus* in the heath had a ratio of 0.75 and in the woodland a ratio of 0.50; *V. vitisidaea,* heath 0.46, woodland 0.26. Cain and Miller (1933), studying *Rhododendron Catawbiense,* found a palisade/sponge ratio of 0.35 for the leaves of plants grown in the contiguous forest of spruce-fir. Although both sponge and palisade were thicker in the heath bald grown leaves than in the forest grown leaves, the palisade was proportionately thicker in the former as shown by the ratios. Duncan (1933) found similar results for *Rhododendron punctatum* grown in the same contrasting habitats, with approximately twice as many rows of palisade cells in the bald grown leaves. The thickness of the palisade tissue was $^4/_5$ more in the heath bald grown leaves in the midvein region of the leaf and $^3/_5$ greater in the leaf margin region than in the forest grown leaves.

Conclusion

In the present study several leaves were taken as a random sample from each plant. The size of the standard deviation in our results is a good indication of the variability encountered as a result of this method. However, the leaves having been so selected, the materials for sectioning and the areas for stomatal frequency and vein length study were always from the same regions of the leaves.

The authors and their students (Cain and Potzger, 1933; Cain and Miller, 1933; Duncan, 1933; with the present paper) have made a contribution to the statistical study of ecological anatomy. They do not mean to suggest by their methods that it is always necessary, or even useful, to employ statistical procedures as in these papers. It is always necessary, however, when contrasts of development between plants of different habitats are to be made, to control rigorously the material selected for study so that it is representative and comparable. There are too many papers in the literature dealing with the comparative ecological anatomy of a species in which the contrasted plant materials are not really comparable, and conclusions as to the effects of habitats are drawn which are not warranted. Although no attempt has been made to survey completely the pertinent voluminous literature on ecological anatomy, enough has been presented to indicate that stomatal frequencies and total vein lengths per unit area, to take an example, vary with the following conditions on a single plant: the size of the mature leaf, the portion of the leaf examined, the height of insertion of the leaf on the stem; the exposure of the leaf (to the north or the south). It follows, then, that to compare these features on plants of the same kind grown under different conditions it is first necessary to select leaves and leaf portions that are strictly comparable. In sunflower, for example,

leaves which are eight or ten nodes apart on the stem of a single plant may show greater tissue differences (the upper being more xeromorphic) than leaves of the same node of two plants, one of which was grown in a xeric habitat and the other in a mesic habitat.

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The Genus Dichelostemma

Robert F. Hoover

Dichelostemma, a genus restricted in its distribution to western North America, comprises several of the species which by various authors have been included in *Brodiaea.* The genus was first recognized by Kunth (1843), who knew only one species. Two additional species were included by Wood (1868). Greene in 1886 applied the name *Brodiaea* to this genus exclusively, assuming that *B. congesta* Smith was the type species of *Brodiaea,* but in 1894 treated the same group as *Dichelostemma* without offering any explanation for his changed opinion. Under the latest International Rules of Nomenclature (ed. 3, p. 144, 1935) the lectotype species of *Brodiaea* is *B. grandiflora* Smith. That generic name must therefore be applied to the group of species treated by Greene (1886) as *Hookera,* and the group now under consideration, if regarded as distinct, must accordingly bear the name *Dichelostemma.*

Probably *Dichelostemma* is more closely related to *Brodiaea* than to any other genus, but study of ample material of all the species of both genera establishes the belief that the two are quite distinct. A summarization of the evidence favoring segregation has been made in a recent article (Hoover, 1939). In the structure of the leaves, which is most easily seen in living plants, is found one of the most impressive differences between *Brodiaea* and *Dichelostemma.* The leaves of *Dichelostemma* are flattened, are keeled on the lower side, and on the upper side show parallel impressions corresponding to the vascular system. Those of *Brodiaea* are narrower, not markedly flattened, never keeled, and have no external indication of veins. The structure of the stigma and style is probably of even greater importance. In *Brodiaea* the stigma at the receptive stage consists of three conspicuous recurving lobes spreading abruptly from the apex of the style. In all species here referred to *Dichelostemma* the style is slightly and gradually enlarged toward the apex by three narrow wing-like projections, each of which terminates in a lobe of the small stigma, which is not expanded beyond the diameter of the apex of the style.

The nature of the rare teratological compound umbels suggests that the inflorescences of the two genera may not be exactly homologous. When the umbel is compound in *Brodiaea,* the scape is branched, bearing two distinct umbels and often additional solitary flowers arising from the same point. An involucre of scarious bracts is found at the branch of the scape and also subtending each of the secondary umbels. In *Dichelostemma* only one species, *D. pulchellum,* is known to produce compound umbels. In such cases the scape is not branched, but one of the pedicels of the primary umbel bears an involucre having the same form and color as a perianth, from which the pedicels of the secondary umbel arise. From these observations, it appears that the involucral bracts of *Brodiaea* may be most closely homologized with

the basal leaves and those of *Dichelostemma* with the perianth-segments. As additional evidence for these homologies, it is notable that all species of *Dichelostemma* show a tendency for the involucre to be colored like the flowers, whereas the bracts in *Brodiaea* show no trace of the blue or violet color of the perianth.

Morphologically, *Dichelostemma* seems to be slightly more advanced than *Brodiaea,* and has for the most part correspondingly higher chromosome numbers, as listed by Johansen (1932). The structure of the stamens is, I am convinced, one of the most important indications of phylogenetic position in this group of plants. All species of *Dichelostemma* except one *(D. pulchellum)* have three of the stamens transformed into staminodia, in this respect resembling *Brodiaea,* but in addition the remaining three stamens are highly modified. The filaments are apparently obsolete, and in some of the species each anther bears two conspicuous wing-like appendages. In *D. pulchellum,* the one species which has six anthers, the stamens opposite the outer perianth-segments have well developed filaments and smaller anthers without appendages, whereas the stamens opposite the inner perianth-segments are of the usual *Dichelostemma* type.

On the basis of flower color, the species of *Dichelostemma* can be divided into two groups. The species with pink or red flowers are distinguished also by having flexuous pedicels which become erect in fruit, while those with blue or violet flowers have straight pedicels which do not change in direction after anthesis. No other constant difference between the two groups has been observed. The red-flowered species all have the perianth-tube six-angled toward the base, but the same condition is seen in *D. congestum* of the blue-flowered group. The two divisions of the genus are so much alike in essential features of flower structure, in fruit, and in vegetative characters that I do not believe any adequate basis for generic segregation exists.

Three different segregate genera of *Dichelostemma* have been proposed by various botanists.

The twining scape of *D. volubile* is so remarkable that three authors independently based a genus on that species (*Macroscapa* Kell., *Rupalleya* Morière, *Stropholirion* Torr.). However, *D. volubile* agrees closely with the other species of *Dichelostemma* in all other vegetative features as well as in flower structure, and no recent author appears to have regarded it as generically distinct.

The segregate genus *Brevoortia,* typified by *D. Ida-maia,* has been rather widely accepted. It possesses three features which might be regarded as generic characters; namely, a bright red perianth, a long perianth-tube, and a stipitate ovary. It is significant, however, that there are intermediate species which constitute a transition to *D. congestum,* the type species of the genus, and thus invalidate the use of such characters as a means of generic distinction. From the bright red color of *D. Ida-maia* there is a transition through the rose-red of *D. venustum* to the pink of *D. volubile,* which is clearly congeneric with the blue-flowered species. *Dichelostemma venustum* is intermediate also in the length of the perianth-tube. The stipe of the ovary, which is

rather conspicuous in *D. Ida-maia,* is short but evident in *D. venustum,* while in *D. volubile* it is obscure if not entirely absent. If *D. venustum* actually is a hybrid between *D. Ida-maia* and *D. congestum,* as some botanists have stated, an additional argument against the generic status of *Brevoortia* is available, for unrelated species can not be expected to hybridize.

The forms with six fertile stamens were segregated by Rydberg (1912) as the genus *Dipterostemon.* Although Rydberg recognized four species, they do not seem specifically distinct from one another and in this revision are all referred to *D. pulchellum.* It is significant that the stamens opposite the inner perianth-segments are like those found in other species of *Dichelostemma,* whereas those opposite the outer segments bear reduced anthers and have well developed filaments, thus corresponding to the staminodia of the other species. In such related genera as *Allium, Bloomeria,* or *Triteleia,* the six anthers are invariably all alike, even though the filaments may be unequal. The important evolutionary development in *Brodiaea* and *Dichelostemma* is not, in my opinion, the complete transformation of the alternate (outer) stamens into staminodia, but rather the reduction of the alternate anthers, regardless of whether or not they become sterile. According to this view, the stamen difference between *Dipterostemon* and *Dichelostemma* is one of degree only, and, because they agree so closely in all other respects, the two groups should not be separated.

The most convincing argument against the division of *Dichelostemma* into smaller genera becomes evident when not only the species directly involved but the members of related genera are considered. It is then seen that those features which are possessed in common by all species of *Dichelostemma* are those which are most important in separating that genus from *Brodiaea* and from other genera less closely related. Such structural features are found in the corm, leaves, bracts, perianth, position of stamens, attachment of anthers, stigma and style, and seeds.

Although certain features of the flowers of *Dichelostemma* are obscured in dried specimens, this fact is not such a cause of confusion among the species as it has been in *Brodiaea.* The flowers retain their distinctive characters sufficiently well to be readily identified. Although there has been some disagreement as to the definition of certain species, all of the species except one are remarkably uniform. Even in the one variable species, *D. pulchellum,* variation does not appear to extend to the structure of the flower.

The chromosome numbers of most species of the genus have been listed by Johansen (1932). The diploid number is said to be 30 in *D. multiflorum,* 36 in both *D. congestum* and *D. volubile,* and 72 in *D. pulchellum* (names here used not in the sense of Johansen, but as in the following revision). It is notable, from the point of view of the definition of the genus, that one of the blue-flowered and one of the red-flowered species have the same chromosome number. *Dichelostemma pulchellum,* or at least the form of that species studied by Johansen, appears to be tetraploid with respect to other members of the genus. In *D. Ida-maia* the chromosome number is said to be variable, but there are usually "close to twenty haploid chromosomes."

While restricted for the most part to the region west of the summits of the Sierra Nevada and the Cascade Range, various species of *Dichelostemma* extend eastward through the gaps of the Columbia, Klamath, and Pit Rivers. This peculiarity of distribution has been noted also with regard to *Brodiaea* and seems to be frequent among the plant genera of western North America. Unlike *Brodiaea*, *Dichelostemma* is not limited to the east by the deserts in southern California but extends eastward to southwestern New Mexico. The center of distribution of *Dichelostemma* can be definitely located in northwestern California, where all species occur and where one is endemic. Only one species is known north of Douglas County, Oregon, and only one occurs in southern California, where it is, however, very common. Probably none of the species is restricted to any particular habitat. The four species with which I am familiar in the field grow successfully in open woods, in grassy meadows, in sun-baked clay, and in dry sandy loam. Vegetative reproduction by means of the formation of a circle of bulblets around the base of the corm normally occurs in all species but appears to be lacking in a rare form of *D. multiflorum*.

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DICHELOSTEMMA Kunth, Enum. Pl. 4:469. 1843

Brodiaea subgenus *Dichelostemma* Eastwood, Bergen's Elements of Botany, Pacific Coast Edition, Key and Flora 20. 1897. *Macroscapa* Kell., Pacific **3**:132. 1854. *Stropholirion* Torr., Pac. R. Rep. **4**:149. 1857. *Rupalleya* Morière, Bull. Soc. Linn. Norm. **8**:317, pl. 15. 1864. *Brevoortia* Wood, Proc. Acad. Philad. **1867**:81. 1867. *Dipterostemon* Rydb., Bull. Torr. Club **39**:110. 1912.

Perennial herbs with scape and leaves arising from a corm. Corm subglobose, with brown fibrous coat, usually producing a circle of bulblets at the base. Leaves 2 to 5, flattened, long-linear, keeled on the lower side, with parallel impressions on the upper side. Scape of fibrous texture, terete, about 2 or 3 mm. in diameter. Flowers in an umbel, each subtended by a bract, the outer bracts of the umbel enlarged, forming an involucre, usually at least partly colored like the perianth. Pedicels jointed to the perianth. Perianth of 6 similar segments and an inflated or campanulate tube about equalling the segments or exceeding them in length (rarely much shorter in depauperate plants). Stamens opposite the outer perianth-segments with reduced anthers or completely transformed into sterile staminodia. Stamens opposite the inner segments with filaments entirely adnate to the perianth, therefore apparently obsolete, and anthers attached at the sagittate base and closely approximate around the style. Style slender, enlarged upward, triangular in cross section, with narrow wings on the angles, each wing terminating in a lobe of the small stigma. Capsule of firm texture, loculicidal, each locule containing two rows

of seeds. Seeds black, elongated, striate-reticulate, triangular in cross section. winged on the angles, narrowed toward each end, with a transverse ridge at the point of maximum diameter.

Type species: *Dichelostemma congestum* (Smith) Kunth.

KEY TO THE SPECIES

Pedicels ascending, not changing direction in fruit; perianth violet or blue (rarely white).
  Pedicels free from one another, all arising from the same point; perianth-tube not angled.
    Perianth constricted at throat; stamens 3, alternating with 3 staminodia; style 7 to 8 mm. long. ..... 1. *D. multiflorum.*
    Perianth not constricted at throat; stamens 6, of two kinds but all bearing anthers; style 4 to 6 mm. long. ..... 2. *D. pulchellum.*
  Pedicels joined toward base, the inflorescence therefore apparently a short dense raceme rather than an umbel; perianth-tube angled toward base.... 3. *D. congestum.*
Pedicels flexuous, spreading or recurved in flower, tending to become erect in fruit; perianth pink to red.
  Scape flexuous, twining; perianth-tube slightly if at all longer than segments.... ..... 4. *D. volubile.*
  Scape rigid, erect; perianth-tube 2 to 3 times as long as segments.
    Perianth uniformly rose-red, the tube 14 to 17 mm. long; style 10 to 12 mm. long. ..... 5. *D. venustum.*
    Perianth with bright red (rarely yellow) tube and green segments, the tube 20 to 25 mm. long; style 15 to 20 mm. long. ..... 6. *D. Ida-maia.*

1. *Dichelostemma multiflorum* (Benth.) Heller, Muhl. 2:15. 1905

Brodiaea multiflora Benth., Pl. Hartw. 339. 1857. *Hookera multiflora* Britten, Journ. Bot. **24**:51. 1886. *Brodiaea grandiflora* Smith var. *brachypoda* Torr., Pac. R. Rep. **4**:149. 1857.

Scape 2 to 8 dm. tall, scabrous or less commonly smooth; bracts ovate, acuminate, purple-tinged toward apex, 7 to 12 mm. long; umbels compact, globose in outline when well developed; pedicels rigid, 3 to 15 mm. long; perianth violet to lilac, the tube 8 to 10 mm. long, inflated, not angled or saccate, thin-membranous after anthesis, becoming cartilaginous in fruit, strongly constricted at the throat, the segments about as long, broadly rounded at apex, rotate at anthesis; staminodia usually white but more or less violet-tinged, broad, involute, 5 to 6 mm. long, entire at apex; filaments entirely adnate, without appendages; anthers 4 to 5 mm. long; style 7 to 8 mm. long.

Josephine County, Oregon, southward in California through the Coast Ranges to Trinity County, the Sacramento Valley to Sacramento County, and the Sierra Nevada to Mariposa County; localized also in San Mateo and Santa Clara Counties, California.

OREGON: Josephine Co.: Grants Pass, 1896, *Gibbons* (UC); Takilma, *Peck 7993* (W); Waldo, *Kildale 7932* (S). CALIFORNIA: Siskiyou Co.: Yreka, *Butler 1361* (P, S, UC); Metcalf's Ranch (northeast base of Mt. Eddy), *Heller 13275* (CA, S). Modoc Co.: Parker Creek, *J. T. Howell 11945* (CA); 6 miles north of Canby, *Applegate 871* (S). Lassen Co.: south side of Dixey Mts., 1894, *Baker and Nutting* (UC); Susanville, 1897, *M. E. Jones* (P). Shasta Co.: Goose Valley, *Eastwood 851* (CA); near Redding, *Heller 7862* (S, UC). Humboldt Co.: Klamath River at Bluff Creek, *Kildale 9752* (S); Hupa Indian Reservation, *Chandler 1310* (S, UC). Trinity

Co.: Weaverville, *Kildale 10761* (S); Hay Fork Mountain, *Tracy 6446* (UC). Tehama Co.: Ely, *Jepson 16339* (J). Plumas Co.: near Greenville, *Heller and Kennedy 8768* (CA, S). Butte Co.: near Cohasset, *Heller 11902* (CA, OS, S); 8 miles north of Oroville, *Heller 11421* (CA, OS, S, UC). Glenn Co.: Orland, *Applegate 5382* (S). Yuba Co.: Los Vergils, *Eastwood 10522* (CA). Nevada Co.: Nevada City, *Eastwood 538* (CA). Sutter Co.: 2 miles north of Union School, *Sindel 54* (VTM). Placer Co.: Emigrant Gap, *Jones 3514* (CA); Blue Canyon, *Walker 1276* (UC). Sacramento Co.: North Sacramento, *Ramaley 11244* (UC). Eldorado Co.: Kyburz, *Belshaw 2345* (VTM); Plum Creek, *Johannsen and Gifford 344* (VTM). Amador Co.: Pine Grove, *Hansen 1073* (S); Antelope, *Hansen 579* (S). Calaveras Co.: Murphy's Camp, *Davy 1501* (UC). Tuolumne Co.: Long Barn, *Hoover 2536* (CA, UC); Big Oak Flat, 1886, *Cleveland* (SD). Mariposa Co.: Fortman Mt., 1895, *Congdon* (UC). San Mateo Co.: San Francisquito Creek, *Hichborn 223* (S). Santa Clara Co.: Stanford University, 1894, *Dudley* (S); San Juan Hills, San Jose, 1895, *Patterson* (S).

This species is comparatively late-flowering and when associated with *D. pulchellum* at low altitudes blooms after that species is in fruit. The inflated perianth-tube and rotate segments give to the flowers of *D. multiflorum* an appearance strongly suggesting miniature hyacinths, so that the common name "Wild Hyacinth," often applied to various members of the genus, is rather appropriate for this species. The globose configuration of the umbels in anthesis (except when unsually few-flowered) is a notable peculiarity.

In its geographical distribution, *D. multiflorum* presents some interesting problems. It is common in the Sacramento Valley of California, especially on the east side, but is unknown in the San Joaquin Valley, perhaps because of reduced precipitation in that region. In the Sierra Nevada it is abundant at altitudes up to 5,000 feet even as far south as Tuolumne County and northern Mariposa County. Although the species is by no means restricted to metamorphic rocks, its range seems to terminate abruptly near the point in Mariposa County where the metamorphic zone of the northern Sierra Nevada foothills is replaced by granite. The apparently localized occurrence of this species in the San Francisco Bay region might be explained by the failure of collectors to obtain it in the intervening territory, but that seems improbable. These localities are equally remote from the Sierra Nevada and from the nearest known localities for the species in the North Coast Ranges. The San Mateo County plants have been observed by the writer in the field and evidently are typical in flower structure, although it was noted that the corms did not bear bulblets as do those of the Sierra Nevada form.

Brodiaea multiflora Benth. and *B. grandiflora* var *brachypoda* Torr. both were based on specimens from the Sacramento Valley, but the exact type locality is not known.

2. *Dichelostemma pulchellum* (Salisb.) Heller, Muhl. 1:132. 1906

Hookera pulchella Salisb., Parad. Lond. under pl. 98; pl. 117. 1808. *Brodiaea pulchella* Greene, Bull. Cal. Acad. **2**:133. 1886. *Dipterostemon pulchellus* Rydb., Bull. Torr. Club **39**:111. 1912. *Brodiaea parviflora* Torr., Pac. R. Rep. **2**:125. 1855. *Hookera parviflora* Torr., Pac. R. Rep. **2**:125. 1855. *Hookera parviflora* Ktze., Rev. Gen. Pl. **1**:711. 1891. *Brodiaea capitata* Benth., Pl. Hartw. 339. 1857. *D. capitatum* Wood (by error Benth.), Proc. Acad. Philad. **1868**:173. 1868.

Milla capitata Baker, Journ. Linn. Soc. **11**:381. 1871. *Hookera capitata* Ktze., Rev. Gen. Pl. **1**:712. 1891. *Dipterostemon capitatus* Rydb., Bull. Torr. Club **39**: 111. 1912. *Brodiaea insularis* Greene, Bull. Cal. Acad. **2**:134. 1886. *D. insulare* Burnham, Muhl. **3**:74. 1907. *Dipterostemon insularis* Rydb., Bull. Torr. Club **39**: 111. 1912. *Brodiaea capitata* var. *insularis* Macbr., Contr. Gray Herb. **56**:9. 1918.

Scape smooth, 1 to 6 dm. tall; bracts ovate to lanceolate, acute or less commonly acuminate, more or less tinged with purple, or often deep purple throughout, 7 to 20 mm. long; pedicels ascending, 1 to 15 mm. long, usually all shorter than the bracts; perianth violet, occasionally varying to white, the tube (3 or) 5 to 8 mm. long, cylindric-campanulate, not at all constricted above, the segments 7 to 11 mm. long, not widely spreading; stamens opposite the outer perianth- segments with triangular -dilated filaments 2 mm. long, the anthers 2 to 3 mm. long; stamens opposite the inner segments with filaments entirely adnate, bearing a narrowly triangular wing 4 to 6 mm. long on either side of the anther, the anthers 3.5 to 4.5 mm. long; style 4 to 6 mm. long.

Douglas County, Oregon, to the middle portion of Baja California; extending east from southern California to southwestern Utah.

OREGON: Douglas Co.: west of Roseburg, *Thompson 2006* (S). Josephine Co.: Grants Pass, 1887, *T. Howell* (S, T, UC, UO); Sexton Mountain, *Henderson 12505* (UO). Jackson Co.: Gold Hill, *Henderson 12262* (UO); Pinehurst, *Applegate 4280* (S). Klamath Co.: Barkley Spring, *Applegate 3541* (S, UC); Anderson Creek, Swan Lake Valley, *Applegate 703d* (S).

CALIFORNIA: Siskiyou Co.: Hornbrook, *Kildale 7767* (S); near Yreka, *Butler 1192* (S, UC). Modoc Co.: Pothole Gulch, *Wilson 42* (VTM). Humboldt Co.: Kneeland Prairie, *Tracy 2674* (UC); Grasshopper Peak, *Constance 914* (WS). Mendocino Co.: Coolidge Redwoods, *Henderson 15449* (UO); South Mill Creek, *Abrams 6946* (S). Glenn Co.: Willows, *Eastwood 10195* (CA). Butte Co.: De Sabla, 1917, *Edwards* (S); 8 miles north of Oroville, *Heller 11778* (CA, OS, S). Sutter Co.: North Butte, *Sindel 26* (VTM); West Butte, *Ferris 691* (S). Colusa Co.: 4 miles east of Williams, *Ferris 521* (S); 5 miles west of Arbuckle, *Ferris 600* (S). Lake Co.: Blue Lakes, *Henderson 15440* (UO); Sulphur Banks, *Bowman 9* (S). Napa Co.: Mt. St. Helena, *C. F. Baker 2612* (UC). Sonoma Co.: near Santa Rosa, *M. S. Baker 701* (UC); 8 miles north of Bay, *J. T. Howell 6428* (CA). Marin Co.: Ignacio, *Abrams 6889* (S); Mt. Tamalpais, *Chandler 487* (UC). Sacramento Co.: Fair Oaks, *Ramaley 11026* (UC). Eldorado Co.: between Shingle Springs and Eldorado, *Heller 12298* (CA, OS, S). Amador Co.: Ione, *Eastwood 10098* (CA). Calaveras Co.: Jenny Lind, 1923, *Baxter* (S). Contra Costa Co.: Mt. Diablo, *Meyer 297* (UC); Point Richmond, *Hoover 2756* (CA, UC). Alameda Co.: Berkeley, *Jepson 7567* (S). San Francisco Co.: Lake Merced, 1901, *K. D. Jones* (UC). San Mateo Co.: Searsville Dam, *Applegate 703b* (S). Tuolumne Co.: Long Barn, *Hoover 2508* (CA, UC); Table Mountain above Rawhide, *Ferris 1481* (CA, S). Stanislaus Co.: 3 miles east of Oakdale, *Abrams 9969* (S); Ceres, 1916, *Wagner* (S). Santa Clara Co.: foothills west of Los Gatos, *Heller 8569* (S); San Martin, *Chandler 919* (UC). Santa Cruz Co.: Arano Gulch, 1902, *C. H. Thompson* (S). Mariposa Co.: Yosemite Valley, *Abrams 4390* (S); Wawona, *J. T. Howell 361* (CA). Merced Co.: 4 miles north of Merced, *Hoover 267* (UC). Madera Co.: Raymond, *Eastwood 12527* (CA). San Benito Co.: Panoche Pass, *Abrams and Borthwick 7990* (S). Monterey Co.: Gigling, *Elmer 4452* (CA, OS, P, S, UC, UO); Pacific Grove, *Heller 6675* (P, S, UC, UO). Fresno Co.: Pine Ridge, *Hall and Chandler 99* (UC); 3 miles north of Reedley, *Hoover 3971* (S, UC); Coalinga, *Eastwood 13454* (CA). Tulare Co.: Goshen, *Eastwood 2920* (CA); Tulare, *Davy 3092* (UC). Inyo Co.: near Willow Creek, Panamint Mts., *Coville and Funston 752* (S); near Lee Well, Nelson Range, *Hall and Chandler 7139* (UC). San Luis

Obispo Co.: Cambria, *Eastwood 13627* (CA); Osos Valley, 1910, *Condit* (UC). Kern Co.: East Bakersfield, *Benson 2983* (S, UC); Randsburg, *Heller 7688* (S, UC). San Bernardino Co.: Vontrigger Spring, *Munz 13668* (P, S, UC); Waterman Canyon, *Parish 11765* (UC). Santa Barbara Co.: 5 miles south of Surf, *Ferris 7518* (S); San Miguel Island, 1930, *Hoffmann* (CA); Valle del Medio, Santa Cruz Island, *J. T. Howell 6194* (CA). Ventura Co.: Lockwood Valley, *Dudley and Lamb 4613* (P, S, UC); Casitas Pass, *Hall 3223* (UC). Los Angeles Co.: Manzana, 1896, *Davy* (UC); Claremont, *C. F. Baker 5241* (P, S, UC); Santa Catalina Island, 1904, *Grant and Wheeler* (S, UC); San Clemente Island, *Munz 6662* (P, UC). Riverside Co.: Banning, *Campbell 51* (CA); Palm Canyon, *Johnston 1077* (S). San Diego Co.: San Diego, *M. E. Jones 3063* (CA, P, S); Yaqui Wells, *Eastwood 2805* (CA).

NEVADA: Nye Co.: Rhyolite, 1907, *M. E. Jones* (P). Clark Co.: Good Springs, 1905, *M. E. Jones* (P). UTAH: Washington Co.: Pine Valley, *Eastwood and Howell 1256* (CA); mesa east of Hurricane, *Maguire and Blood 1307* (UC); Zion Canyon, 1923, *M. E. Jones* (P). ARIZONA: Mohave Co.: White Hills, 1903, *M. E. Jones* (P); Stockton Hill road near Kingman, 1927, *Braem* (S). Pima Co.: foothills, west side of Baboquivari Mts., *A. and R. A. Nelson 1159* (UC). BAJA CALIFORNIA: Cabo Punta Banda, *Wiggins 4235* (P, S, UC); San Telmo, 1893, *T. Brandegee* (UC); San Martin Island, *Anthony 222* (S, UC); Guadalupe Island, 1897, *T. Brandegee* (UC); San Benito Island, 1897, *T. Brandegee* (UC); Cedros Island, 1897, *T. Brandegee* (UC).

This species is the most widely distributed of the genus and is very abundant over large areas, especially in California. At low altitudes it is one of the earliest spring flowers, but where it occurs in the mountains, its flowering season coincides with that of *D. multiflorum*. In depauperate plants the perianth-tube is often very short.

The original figure of *Hookera pulchella* Salisb. clearly represents this species and not *D. congestum*, to which that name has usually been applied. The flower is shown as having six anthers, three of them with the two wing-like appendages which characterize the present species. The illustration of the corm also is more representative of this species than of *D. congestum*. Some authors, notably Greene (1886), have attempted to distinguish two hexandrous species, but in the course of the present study it has been impossible to discover any basis for separating *D. capitatum* from *D. pulchellum*.

There has also been some doubt as to the application of the name *Brodiaea parviflora* Torr. It has usually been considered as identical with *D. multiflorum*. No authentic material has been seen by me, but the first collection cited, which presumably should be considered the type, was collected by Fremont in Utah. Assuming that this collection actually belongs to the genus *Dichelostemma* and was accompanied by correct data, it could hardly belong to any species but *D. pulchellum*, because no other species of the genus is known to occur in Utah.

The corms of *D. pulchellum* are unique in bearing bulblets on short offsets, not directly on the base of the corm as in the other species. The bulblets thus have more space in which to develop and are rounded rather than long and slender. This feature of the corms makes it possible to recognize living plants of the species at any stage of development, but it is usually of no value in the identification of dried specimens. Apparently long fragile offsets, in addition to the bulblets at the base of the corm, may occur in other

species, especially in *D. Ida-maia*, but it is difficult to demonstrate the existence of such offsets even in living plants.

Dichelostemma pulchellum shows the range of variation which would be expected in a species of such wide geographical distribution. Particular mention should be made of *Brodiaea insularis* Greene, a variant occurring on the islands off the coast of southern California and northern Baja California. This plant seems to differ from typical *D. pulchellum* only in having very tall scapes and very large leaves. Field observations lead me to believe that these differences are without taxonomic significance. In favorable situations, such as fertile creek bottoms, and in seasons with favorable weather conditions, plants of the mainland may sometimes grow as large as any of the specimens seen from the islands. There is probably a genetic basis for the size of the insular plant, but since the same form may apparently be produced under the direct stimulus of environment, segregation on such a basis does not seem desirable.

The collections from Nevada and Utah do not differ appreciably from the prevailing form of the species in California, but in western Arizona and to a smaller degree in southeastern California the plants tend to exhibit some of the features of the following variety. Here are cited a few specimens which are so exactly intermediate that I am unable to refer them definitely either to typical *D. pulchellum* or to the variety.

ARIZONA: Mohave Co.: Hackberry, 1903, *M. E. Jones* (P); Kingman, *Eastwood 18009* (CA). CALIFORNIA: San Bernardino Co.: Bonanza King Mine, *Munz, Johnston, and Harwood 4030* (P). Riverside Co.: Andreas Canyon, 1917, *Johnston* (P).

2a. **Dichelostemma pulchellum** (Salisb.) Heller var. **pauciflorum** (Torr.) comb. nov.

Brodiaea capitata Benth. var. *pauciflora* Torr., Bot. Mex. Bound. 218. 1859. *Milla capitata* (Benth.) Baker var. *pauciflora* Baker, Journ. Linn. Soc. **11**:381. 1871. *D. pauciflorum* Standl. Contr. U. S. Nat. Herb. **13**:179. 1910. *Dipterostemon pauciflorus* Rydb., Bull. Torr. Club **39**:111. 1912. *Hookera pauciflora* Tidestrom, Contr. U. S. Nat. Herb. **25**:123. 1925.

Bracts ascending, lanceolate to linear-lanceolate, acuminate, white-scarious, with little or no tinge of purple; pedicels slender, mostly surpassing the bracts, 6 to 35 mm. long; perianth-segments apparently widely spreading.

Northwestern Arizona and southwestern New Mexico to northern Sonora, recurring on the western border of the Colorado Desert in southern California and represented in the intervening region by apparently intermediate forms.

ARIZONA: Mohave Co.: Yucca, 1884, *M. E. Jones* (P). Yavapai Co.: Clemenceau, 1922, *W. W. Jones* (UC); Skull Valley, 1903, *M. E. Jones* (P). Gila Co.: Sierra Ancha, *Eastwood 17580* (CA); Roosevelt Dam, *Eastwood 6209* (CA); San Carlos, 1932, *Ethel Palmer* (CA). Maricopa Co.: Aguila, *M. E. Jones 25920* (P, S); Morristown, *Gillespie 5362* (P, S); 9 miles north of Apache Junction, *Abrams 12963* (S). Pinal Co.: Superstition Mt., *Beckett 10776* (P). Greenlee Co.: Duncan, 1920, *Durant* (P). Pima Co.: Tumamoc Hill, Tucson, *Keck 3000* (S, UC); below Range Reserve Station, Santa Rita Mts., *Graham 3026* (S). Cochise Co.: Silver Creek, 1928, *Ballou* (P, S); Warren, 1915, *Carlson* (CA). Santa Cruz Co.: Nogales, *Fosberg 7822* (P). NEW MEXICO: Grant Co.: Mangas Springs, *Metcalfe 41* (P, S, UC); Silver City, *Eastwood 8425* (CA). Hidalgo Co.: Lordsburg, *M. E. Jones 25921* (P). CALIFORNIA: Riverside Co.: Agua Caliente (now Palm Springs), *Parish 364* (S); Tah-

quitz Canyon, *M. S. Baker 2807b* (S); Murray Canyon, 1926, *Ballou* (S). San Diego Co.: Warner Hot Springs, 1913, *Eastwood* (CA) (bracts purple, but otherwise corresponding to var. *pauciflorum*). SONORA: 30 miles south of Nogales, *Abrams 13147* (S); 4 miles south of Imuris, *Abrams 13201* (S).

None of the differences between this variety and typical *D. pulchellum* appears to be constant. It seems probable that the perianth-segments in the variety may be rotate or reflexed at anthesis, but that feature can be seen only in exceptionally well preserved herbarium specimens. Field study of var. *pauciflorum* and the apparently intermediate forms is greatly needed. On the basis of the information at present available, however, it is impossible to place any definite line of division. The original collection of *Brodiaea capitata* var. *pauciflora* Torr. was made by Bigelow near the "Copper Mines" in Grant County, New Mexico.

3. *Dichelostemma congestum* (Smith) Kunth, Enum. Pl. 4:470. 1843.

Brodiaea congesta Smith, Trans. Linn. Soc. **10**:3, pl. 1. 1811. *Hookera congesta* Jepson, Fl. West. Mid. Cal. 116. 1901.

Scape 3 to 9 dm. tall; bracts light purple, ovate-acuminate, 10 to 15 mm. long; umbel very compact, with pedicels shorter than the bracts; pedicels ascending, not arising from the same point but joined toward the base in such a manner as to form a short erect peduncle-like projection above the involucre, the free portion of the pedicels 1 to 6 mm. long; perianth blue-violet, the tube 8 to 10 mm. long, six-angled, a little constricted at the throat, the segments about equalling the tube, not widely spreading; staminodia 5 to 6 mm. long, deeply bifid at apex, the midvein entirely adnate to the perianth and commonly produced into a short point between the two lobes; filaments entirely adnate; anthers linear, 4 to 5 mm. long; style 5 to 6 mm. long.

Island County, Washington, to Santa Clara County, California.

WASHINGTON: Island Co.: Whidby Island, *Gardner 283* (WS). Kitsap Co.: Waterman, *Warren 117* (WS). King Co.: Alki Point, 1889, *Piper* (UW). Pierce Co.: Lake Steilacoom, 1928, *Owen* (WS). Thurston Co.: Granger's Prairie, 1905, *Townsend* (WS). Clarke Co.: East Mill Plain, *English 1081* (WS); Fourth Plain, 1899, *Piper* (WS). Klickitat Co.: Bickleton, 1927, *Gotfredson* (P); Goldendale, *Thompson 11536* (P, S, UW).

OREGON: Wasco Co.: Siwash Flat, *Thompson 4208a* (T); The Dalles, 1928, *Hungate* (WS). Hood River Co.: Hood River, *Peck 1354* (W), 1880, *Henderson* (UO). Multnomah Co.: Sauvie's Island, *Henderson 963* (OS). Washington Co.: Scroggins Creek, *Thompson 4287* (S); near Forest Grove, *Thompson 861* (S, T). Clackamas Co.: Willamette Falls, *Sheldon 12242* (UO); near Estracada, *Thompson 2614* (S). Marion Co.: Salem, *Peck 1355* (W); Breitenbush, *Peck 16262* (W). Linn Co.: Crabtree, 1915, *Hatch* (OS); Sweet Home, *Henderson 13599* (UO). Benton Co.: Corvallis, *Gilbert 484* (US). Lane Co.: near Florence, *Henderson 16394* (UO); 3 miles south of Cottage Grove, *Peck 14930* (W). Douglas Co.: near Riddle, *Gale 193* (S). Curry Co.: Agness, *Applegate 7141* (S); near Brookings, *Henderson 7205* (UO). Josephine Co.: 9 miles north of Grants Pass, *Eastwood and Howell 2805* (CA); Mt. Grayback, *Thompson 12967* (T, W, WS). Jackson Co.: Pinehurst, *Applegate 4384* (S); Little Chinquapin Mountain, *Applegate 4294* (S, UC). Klamath Co.: Clover Creek near Buck Lake, *Applegate 704b* (S); Cherry Creek, *Applegate 6059* (S).

CALIFORNIA: Siskiyou Co.: Shasta Springs, *Eastwood 11958* (CA). Shasta Co.: Fall River Springs, *Hall and Babcock 4192* (P, UC). Humboldt Co.: Table Bluff, *Tracy 6375* (UC); Dinsmore's Ranch, *Tracy 4144* (UC). Mendocino Co.: Round

Valley, *Goddard 607* (UC); Potter Valley, *Eastwood 12632* (CA). Butte Co.: Little Chico Creek, *R. M. Austin 40* (UC); near Clear Creek, *Brown 211* (S). Colusa Co.: Sycamore Slough, *Ferris 6309* (S). Lake Co.: 2 miles west of Hough's Springs, *Abrams 12503* (S); Cobb Mountain, *M. S. Baker 2288a* (UC). Napa Co.: 5 miles east of St. Helena, *Bacigalupi, Ferris, and Wiggins 6658* (S, UC). Sonoma Co.: Independence School, near Healdsburg, *Abrams 6907* (S); Petaluma, *Eastwood 10437* (CA). Sacramento Co.: Fair Oaks, *Ramaley 11299* (UC). Solano Co.: Vacaville, *Jepson 6796* (J). Marin Co.: Ignacio, *Abrams 6895* (S). Contra Costa Co.: Mt. Diablo, *Eastwood 4474* (CA); St. Mary's College, *J. T. Howell 11258* (CA). Alameda Co.: Berkeley, 1884, *Greene* (S, UC). Santa Clara Co.: Stanford University, *Abrams 2376* (S); Stevens Creek, *Pendleton 758* (UC); Smith Creek at foot of Mt. Hamilton, *Heller 8587* (S, UW); Coyote Creek canyon, *Dudley 4119* (S).

Dichelostemma congestum extends much farther north than any other species of the genus. In California it is nearly restricted to the Coast Ranges but has been found at a few localities on the east side of the Sacramento Valley. The species was originally collected by Menzies in 1792 in "New Georgia." The figure accompanying the original description of *Brodiaea congesta* is sufficiently detailed to leave no doubt as to the application of the name. Many authors have identified this species with *Hookera pulchella* Salisb., but that name seems to belong properly to the preceding species.

4. *Dichelostemma volubile* (Kell.) Heller, Bull. S. Cal. Acad. 2:65. 1903.

Macroscapa volubilis Kell., Pacific **3**:132. 1854. *Rupalleya volubilis* Morière, Bull. Soc. Linn. Norm. **8**:317. 1864. *Brodiaea volubilis* Baker, Journ. Linn. Soc. **11**:377. 1871. *Hookera volubilis* Jepson, Fl. West. Mid. Cal. 116. 1901. *Stropholirion californicum* Torr., Pac. R. Rep. **4**:149. 1857. *D. californicum* Wood, Proc. Acad. Philad. **1868**:173. 1868. *Brodiaea californica* Jepson, Fl. West. Mid. Cal. ed. 2, 101. 1911 (not *B. californica* Lindl.).

Scape 4 to 15 dm. long, flexuous and twining, the terminal portion erect; bracts ovate, acute, 10 to 15 mm. long, pink-tinged; pedicels slender, 1 to 4 cm. long, flexuous and spreading or drooping at anthesis, curving upward in fruit; perianth light pink to rose-pink, the tube about 5 mm. long, inflated, strongly six-angled and saccate, the segments 5 to 7 mm. long, rotate at anthesis, becoming erect and approximate in fruit; staminodia white, linear-oblong, 2.5 to 3 mm. long, bifid at the obtuse apex, the margin denticulate; filaments entirely adnate to perianth, at apex bearing two oblong white appendages which nearly equal the anther; anthers linear, 3 to 4 mm. long; style 3 to 4 mm. long; capsule obscurely short-stipitate or quite sessile.

California, in the inner Coast Ranges from Tehama County to Solano County or perhaps Contra Costa County, and in the Sierra Nevada foothills from Butte County to Kern County.

CALIFORNIA: Tehama Co.: foothills above Paskenta, *Hoover 4103* (CA, S). Mendocino Co.: trail to Osborne's, Forest Reserve, *Eastwood 15231* (CA); East Eel River, 1884, *Rattan* (S). Colusa Co.: Williams—Stonyford road, *Ferris 6413* (S); near Wilbur Springs, *Keck 2400* (P, S). Lake Co.: near Grizzly Springs, *Eastwood and Howell 5610* (CA). Napa Co.: Zem Zem, *Jepson 9048* (J). Yolo Co.: Capay Valley, 1891, *Lemmon* (UC). Solano Co.: Mix (Weldon) Canyon, *Hoover 3184* (UC). Contra Costa Co.: Mt. Diablo, "1893?", *Dudley* (S) (record needs confirmation). Butte Co.: Cana, *Hoover 1171* (CA); 2 miles below Centerville, *Heller 11848* (CA, OS, S). Yuba Co.: Stanfield Hill, *Wolf 8778* (UC). Placer Co.: near

Auburn, 1891, *Sonne* (UC). Eldorado Co.: New York Ravine, 1907, *K. Brandegee* (UC). Amador Co.: near Plymouth, *Gross 182* (S); Caminetti Ranch near Jackson, *Mulliken 103* (P, S, UC). Calaveras Co.: near Burson, *Stanford 241* (WS); near Copperopolis, *Davy 1347* (UC). Tuolumne Co.: Columbia, 1915, *A. L. Grant* (UC); Spring Gulch, *Williamson 38* (CA, P, S). Mariposa Co.: Hell Hollow, 1929, *Branson* (CA); near Wawona, *J. T. Howell 403* (CA). Madera Co.: Coarsegold, *Benson 3578* (S). Fresno Co.: Pine Ridge, *Hall and Chandler 80* (UC); Kings River above Piedra, *Hoover 3987* (UC). Tulare Co.: near Coffeepot Camp, *Dudley 1791* (S); 3 miles west of Three Rivers, *Bacigalupi 1190* (S). Kern Co.: Guerrilla Flat (vicinity of Poso Creek Valley), *Dudley 556* (S).

In the chaparral belt of the Sierra Nevada foothills, *Dichelostemma volubile* is often one of the most conspicuous components of the flora. It climbs on bushes and is most plentiful in areas which have been recently burned over. In the Coast Ranges it occurs more sparingly. The occurrence of this species in the Sacramento Valley at Cana, Butte County, suggests that the two parts of its range are connected to the north.

Where *D. volubile* and *D. multiflorum* were growing close together under cultivation, a single plant appeared which was apparently a hybrid. The flowers were lilac in color but shaped like those of *D. volubile*, and the scape was weak and flexuous but not twining. Such interspecific hybrids may account for the statement by some authors that the flowers of *D. volubile* are occasionally "purplish-blue" (Curran, Bull. Cal. Acad. 1:149) or "violet" (Greene, 1886). In all specimens of this species which I have seen, the flowers are some shade of pink. I have been unable to find twining scapes in any other species of *Dichelostemma*, although the tortuosity of the scape has sometimes been regarded as a distinctive character of this genus, as by Greene (1886). Possibly there are occasional hybrids which combine twining scapes with the flower characters of species other than *D. volubile*.

5. **Dichelostemma venustum** (Greene) comb. nov.

Brevoortia venusta Greene, Pitt. **2**:230. 1892. *Brodiaea venusta* Greene, Pitt. **2**:250. 1892.

Scape 4 to 9 dm. tall; involucral bracts ovate-lanceolate, acute or acuminate, scarious but more or less tinged with rose-color; pedicels flexuous, becoming erect in fruit, slightly or not at all exceeding the bracts, 1 to 2 cm. long; perianth rose-red, the tube distended-cylindric, 14 to 17 mm. long, angled and saccate at the base, the segments spreading at anthesis, 7 to 8 mm. long; staminoda white or pink-tinged, 3 to 3.5 mm. long, as broad as or broader than long, rounded at apex, apparently somewhat involute; filaments apparently obsolete, each anther at its point of attachment to the perianth apparently joined to the staminodia on either side; anthers 5 to 6 mm. long; style 10 to 12 mm. long; capsule with a very short stout stipe.

Northwestern California from Del Norte County to Trinity County; very rare.

CALIFORNIA: Del Norte Co.: 3 miles northwest of Requa, 1921, *McGregor* (S). Siskiyou Co.: Highland Mine, *Butler 889* (S, UC). Humboldt Co.: valley of South Yager Creek, *Tracy 6524* (UC); Buck Mountain, *Tracy 4351* (UC). Trinity Co.: Island Mountain, 1928, *E. R. Leach* (CA).

The characters of *Dichelostemma congestum* and *D. Ida-maia* are so combined in this species as to suggest a hybrid origin. Mr. Carl Purdy was the first to suggest that it is a hybrid between those two species, having been quoted to that effect by Greene (1892), and has stated in a letter to me that he is still of the same opinion, although he knows of no attempts to produce *D. venustum* experimentally. The same opinion has been expressed by Mr. M. S. Baker (1929) and by Mr. J. P. Tracy (in note accompanying herbarium specimen). On the other hand, Johansen (1932) states that it is "indubitably a hybrid between the valid species [*D. Ida-maia*] and *Dichelostemma capitatum*." The observations of botanists who know this plant in the field are not to be ignored, but it appears that *D. venustum* may occur where the other species are absent. At the Highland Mine in Siskiyou County, none of the three species which have been suggested as possible parents is known to occur, although another species, *D. multiflorum*, has been collected at the same locality. The hybrid origin of *D. venustum*, although highly probable, is therefore not a matter of certainty.

Assuming that this plant actually is a hybrid between *D. congestum* and *D. Ida-maia*, there is no apparent reason for not regarding it as a valid species. It does not exhibit fluctuating variation between the two parent species but in the few localities where it is known always appears in identical form. Whatever its origin may have been, it is now sharply set off from all other species by constant morphological characters. The recognition of *D. venustum* as a species therefore does not depend on the outcome of experiments designed to produce the plant by hybridization, although such experiments would naturally be of great interest.

The record of the occurrence of this species in Mendocino County published by Jepson (1922) and subsequently by Abrams (1923) is based on an incorrect identification, the cited collection from Orr's Springs being *D. Ida-maia*.

6. *Dichelostemma Ida-maia* (Wood) Greene, Man. Reg. S. F. Bay 318. 1894.

Brevoortia Ida-maia Wood, Proc. Acad. Philad. **1867**:82. 1867. *Brodiaea Ida-maia* Greene, Pitt. **2**:250. 1892. *Brodiaea coccinea* Gray, Proc. Am. Acad. **7**:389. 1868. *Brevoortia coccinea* Wats., Proc. Am. Acad. **14**:239. 1879.

Scape 3 to 9 dm. tall; bracts oblong-lanceolate, 15 to 25 mm. long, narrowed above but obtuse at the very apex, more or less red-tinged; pedicels mostly exceeding the bracts, 1 to 5 cm. long, flexuous and somewhat pendulous at anthesis, curving upward in fruit so that the withered perianth stands erect; perianth-tube bright red, 20 to 25 mm. long, somewhat angled and saccate at the base, cylindric at anthesis, becoming inflated in fruit; perianth-segments light green above the red base, ovate-lanceolate, 7 to 9 mm. long, recurved at anthesis, becoming connivent in fruit; staminodia white, broader than long, involute, rounded at apex, 3 to 4 mm. long; anthers 6 to 8 mm. long; style 15 to 20 mm. long; ovary with a stout stipe about half as long as the body.

Curry County, Oregon, to Mendocino County, California, extending east to Shasta County, California.

OREGON: Curry Co.: Brookings, *Henderson 7204* (UO); Harbor, *Peck 8796* (W). Josephine Co.: alpine slopes back of Oregon Caves, *Thompson 12947* (T, W, WS). CALIFORNIA: Del Norte Co.: near Requa, 1899, *Dudley* (S); coast 2 miles north of Humboldt County line, *Keck and Clausen 3399* (S); Wilson Creek, *Abrams and Bacigalupi 8330* (S). Humboldt Co.: Brannan Mountain, *Tracy 3438* (UC); near Alder Point, *Eastwood and Howell 4729* (CA). Shasta Co.: McCloud River near Pitt, *L. E. Smith 263* (CA); Trinity Divide, 1896, *Blasdale* (UC). Trinity Co.: Island Mountain, 1928, *E. R. Leach* (CA). Mendocino Co.: Bell Springs, *Abrams 5945* (S, T); divide of Russian and Eel Rivers, *Bolander 6560* (CA, UC); Orr's Hot Springs, *Ehlers 467* (UC). Lake Co.: 4 miles northeast of Hunter Point, *Simontacchi 249* (VTM). Contra Costa Co.: near Mt. Diablo, 1893, *E. E. Smith* (S) (probably incorrectly labelled).

This very showy species, to which is frequently applied the appropriate common name "Firecracker Flower," is restricted in distribution and probably does not extend farther south in California than Mendocino County. The record of its occurrence in Marin County published by Greene (1894) without citation of a definite locality or collection and repeated by subsequent authors in stating the range of this species is probably erroneous. No specimens from Marin County have been seen, and such a conspicuous plant would hardly be overlooked. Mr. Milo S. Baker, who is well acquainted with the flora of Sonoma County, tells me that he does not know of its occurrence there. It is likewise very improbable that the cited specimen said to have been collected in Contra Costa County is accompanied by correct data, although Contra Costa County was included in the range of the species by Abrams (1923) on the basis of this collection. If present in that vicinity, this species could hardly have escaped the notice of the many botanists who have visited the Mt. Diablo region in recent years.

Dichelostemma Ida-maia is a choice flower for the garden, although it is seldom seen in cultivation. Because of its striking appearance, it is often regarded as a distinct genus, *Brevoortia,* but the recognition of such a genus can not be justified by a consideration of morphological characters, as has been pointed out in the generic discussion above.

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Physical Profiles of the Ozark Province

Arthur B. Cozzens

From the standpoints of the ecologist and geographer, the Ozark Province is one of the less known parts of the United States, despite widespread interest in this area among the students of both sciences. Numerous papers discuss limited parts and aspects of the Ozarks and a few, among which the works of Sauer[1] and Schottenloher[2] are notable, use the regional approach. There is, however, a definite need for a thorough analysis on a regional basis of the fundamental relationships among the factors of the physical environment. Such a study has been in progress for several years, and some of the results have been published in a recent article,[3] including a number of maps based

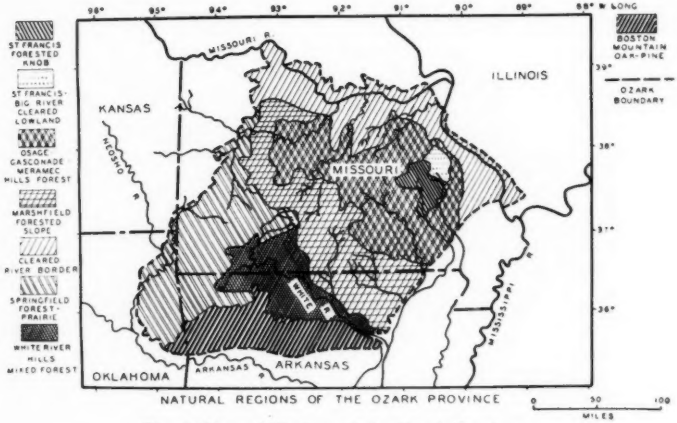

Fig. 1. Natural Regions of the Ozark Province.

on quantitative data. The present paper supplements this earlier article by emphasizing the details of the natural landscape complexes. Together, these papers are designed to constitute a basis for further studies of Ozark ecology and geography.

To facilitate the recognition of relationships, material is here presented by

1 Carl O. Sauer, The Ozark Highland of Missouri, Univ. of Chicago Press, 1920.

2 Rudolph Schottenloher, Ozarkland, *Amerikanische Landschaft*, Erich von Drygalski, editor, Berlin, 1936, pp. 1-125.

3 Arthur B. Cozzens, Analyzing and Mapping Natural Landscape Factors of the Ozark Province, *Trans. Acad. Sci. of St. Louis* **30**(2), May, 1939.

means of generalized physical profiles and supplementary descriptions Also those phases of the geology which are significant elements of the regional geographic complexes and which, therefore, should prove useful to other students of the Ozark Province are outlined in the appendix to this paper. Each of the natural regions shown in Fig. 1 is represented in Figs. 2, 3 and 4 by one or more idealized profiles. These diagrams depict typical conditions and rarely show individual features; for example, escarpments commonly are not represented because of their limited areal extent. Horizontal and vertical scales indicated at the base and left side of each diagram, as in Fig. 2, permit the representation of the average width of the hills[4] and of the local relief (here taken to be the difference in elevation between the summit of a hill and the lowest point of contact between the slope and a bounding drainage line or level lowland).[5] Zero on the vertical scale marks the base of the slope, from which the measurements are made, and the other values above it represent the limits of the local relief within the region, as 200 feet (minimum) to 300 feet (maximum). Some profiles display three relief values, the lowest referring to inferior hills associated with the higher.

Regional Descriptions

The St. Francis Forested Knob Region, Figs. 1 and 2A, is an area of high, rounded knobs of felsite porphyry and granite, separated by basins developed on weak, non-cherty sedimentary rocks. Local relief of 500 to 900 feet[8] reflects the high differential resistance[9] between the igneous rocks, rock type 1 (+)[10] and the strata, rock type 2 (—). In the basins, the relief is generally less than 200 feet, but a few steep-sided ridges capped by cherty limestone, rock type 3 (+), rise nearly 300 feet above bounding drainage lines. More than 75 per cent of the area is in slopes steeper than 14 per cent.[11] The

4 The term *hills*, as here used, refers alike to knobs (isolated elevations), to ridges and to gently sloping minor interstream areas with elongated summits, for which the name *swell* is proposed.

5 For each ridge or swell, several relief measurements were made, the points of maximum elevation in each instance being located within a part of the hill delimited by minor drainage lines on the slopes and having a more or less independent summit.

7 John L. Ridgeway, The Preparation of Illustrations for Reports of the United States Geological Survey, Government Printing Office, 1920; reference is to Plate 3.

8 For further physiographic measurements see Cozzens: op. cit.

9 Differential resistance is the qualitative expression of the difference in the abilities of adjoining rock masses to withstand weathering and erosion.

10 Rock type numbers refer to the lithic units designated in Figure 5 and the accompanying description. Plus and minus signs indicate the resistance relationships between any two adjoining rock masses; plus designates the positive, more resistant member of the pair, minus, the negative, less resistant. These terms are relative; hence, a stratum may be positive with respect to the underlying bed and negative to the overlying.

11 The slope values, "steeper than 14 per cent" and "steeper than 5 per cent," were chosen to indicate the large amount of rough land in the Ozark Province; they are related, in general, to land use. Slopes exceeding 14 per cent commonly are left in tim-

ber, whereas those exceeding 5 per cent include both the timber lands and the areas best suited for cleared pasture. Percentages of land suitable for crops or for cleared pasture, only, may be computed from the other values. The percentages of land in the different slopes were determined for areas of similar physiography previously outlined, not for the region as a unit.12

12 Cozzens, op. cit. pp. 51 and 56.

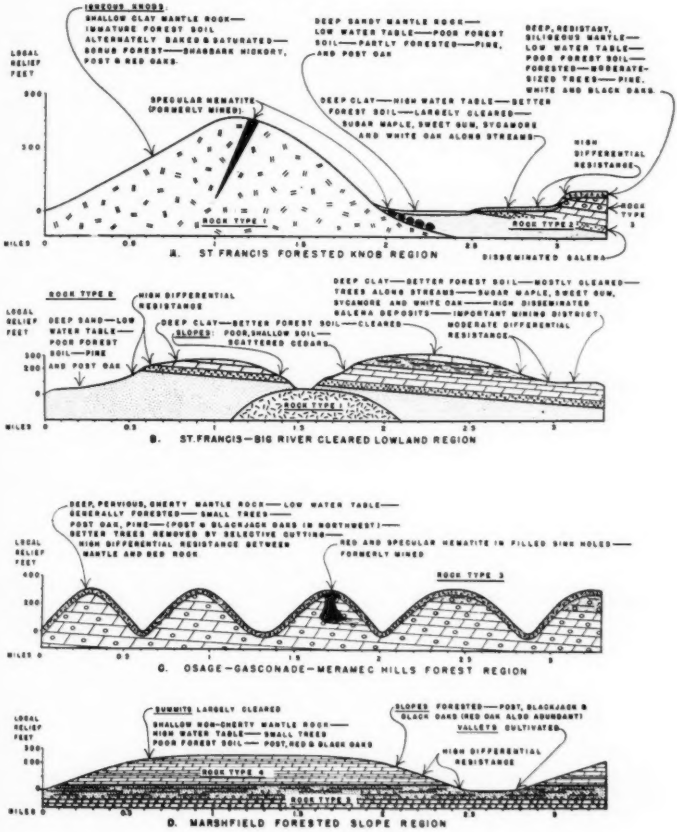
A. ST FRANCIS FORESTED KNOB REGION
B. ST.FRANCIS—BIG RIVER CLEARED LOWLAND REGION
C. OSAGE—GASCONADE—MERAMEC HILLS FOREST REGION
D. MARSHFIELD FORESTED SLOPE REGION

Fig. 2. Physical Profiles I.6

6 The rock types designated in the profiles above and referred to throughout the article were established as a part of this study; they are described in the appendix. In all the profiles and in the rock column, Figure 5, the lithology is indicated by standard symbols.7

igneous knobs are circular to eliptical in plan and average two miles in width at the base.

On the steep slopes of the knobs shallow clay mantle rock and immature forest soils have developed. Due to the thin residuum and impervious bed rock, the soil is alternately saturated and baked. These conditions have resulted in a scrub forest in which shagbark hickory *(Carya ovata)*, post oak *(Quercus stellata)* and red oak *(Q. borealis)* are the predominant species;[13] that is, they collectively constitute more than half of the stand. The names of the predominant species are listed in order of decreasing abundance. The woods vary considerably in size and composition in different sites. On narrow summits the trees are smallest with shagbark hickory and post oak predominant, whereas on extensive summits and on slopes the trees are moderate-sized and shagbark hickory, black and red oaks make up more than 50 per cent of the stand. Red oak appears to be localized by fractures in the bed rock which supply relatively dependable soil moisture. Very little of the land underlaid by igneous rock is cultivated, but considerable areas were cleared, partially or entirely, several times during the nineteenth century to supply fuel for pioneer iron and lead furnaces.

In the lowlands slight erosion and rapid weathering of the weak sedimentary rocks have resulted in the development of deep mantle rock which consists of sands on the sandstone and clays on the dolomite, limestone and shale. The clays, which hold moisture well, have developed good forest soils; hence, the areas in which they occur have been largely cleared for cultivation. Woods are restricted almost entirely to stream margins, where sugar maple *(Acer saccharum)*, sweet gum *(Liquidambar styraciflua)*, white oak *(Q. alba)* and sycamore *(Platanus occidentalis)* are predominant. In the sandy areas, with their low water tables and poor forest soils, much of the land has been cleared, although only a small part of this is cultivated. In the woods which remain, pine *(Pinus echinata)* and post oak predominate.

Iron and tungsten ores formerly were mined from the igneous rocks, as were lead, nickel and cobalt from the sedimentary strata. The deposits, however, are too low grade to warrant production at present prices.

The St. Francis-Big River Cleared Lowland Region, Figs. 1 and 2b, is a topographic basin developed on rock type 2 (—) and inclosed on the west, north and east by an escarpment capped by rock type 3 (+). Despite moderate differential resistance of the strata, a local relief of 200 to 300 feet has developed, because the rocks commonly decrease in resistance from top to bottom, each positive formation exerting a capping effect on the negative beds below. However, where a single formation occurs at the surface over a considerable area, the differential resistance is low and the slopes are gentle.

13 The term predominant is substituted for dominant, previously used (Cozzens, op. cit.), to conform to the usage of the American Society of Foresters.[14]

14 Amer. Soc. of Foresters, Forest Cover Types of Eastern United States, *Journ. of Forestry* **30**:451-498, 1932, reference is to p. 455.

Less than 25 per cent of the land of the entire region is in slopes steeper than 14 per cent and from 25 to 50 per cent is in slopes steeper than 5 per cent. The average width of the swells and ridges is about one and one-half miles.

Soils formed from the non-cherty limestone and shaly dolomite are among the best in the Ozarks, but those from the sandstone are poor. Creek margins have been left in timber resembling that in similar locations in the preceding region, and some sandstone areas still retain woods in which pine and post oak comprise more than half the trees; the remainder of the land is cultivated.

Within the region, in the Bonneterre dolomite, are the important disseminated lead deposits of southeast Missouri.

The Osage-Gasconade-Meramec Hills Forest Region, Figs. 1 and 2C, is an area of steep-sided ridges averaging .7 mile in width, carved from near-horizontal strata by the closely spaced tributaries of dendritic streams. Differential resistance is high between deep siliceous residuum (+) and the underlying sedimentary rocks, rock type 3 (—); it is moderate to high between the Roubidoux sandstone (+), which is the upper unit of rock type 3, and the cherty dolomites (—) below. The capping effect thus produced has resulted in local relief of 200 to 400 feet and in high angles of slope. In the central part of the region more than 75 per cent of the land is in slopes steeper than 14 per cent; and in most of the entire region 75 to 100 per cent of the land is in slopes steeper than 5 per cent. However, on uplands remote from major drainage lines, where the Roubidoux sandstone is continuous, differential resistance is lower, as are land slopes and local relief.

Because of well developed drainage through caverns and through the deep, pervious mantle rock, the water table is low, expect in the valleys, in which there is a marked underflow through the residuum. Due to the recurrent deficiency of soil moisture, the woods on hilltops and slopes consist of small trees. In contrast to these, the woodlands of the valley floors are composed of moderate-sized trees and closely resemble those which fringe the streams in the regions previously described. Only the valley bottoms and occasional hilltops are cleared for agriculture, the rest of the area being unsuitable for cultivation because of its steep slopes. On the hills, post oak and pine are predominant in the southeastern part of the region, and post oak and blackjack oak *(Q. marilandica)* in the northwestern. Pine is absent from the latter area except where planted, which lack may be due in part to the proximity of the climatic limit of the species; probably, however, it is chiefly the result of an edaphic barrier, a narrow strip of dolomite, rock type 4, which entirely spans the region. The small size of the timber reflects the extremely slow growth of the post and blackjack oaks and the repeated cutting of trees for lumber and for fuel for pioneer iron furnaces.

Ore for the pioneer furnaces was obtained from local deposits of red and specular hematite which occupy filled sink holes. The better ore bodies have been exhausted and the others are not being workd at present as a result of low prices. Barite, which occurs in the deep mantle rock formed from the

Potosi dolomite, is now the only mineral of nation-wide economic importance in the region.

The Marshfield Forested Slope Region, Figs. 1 and 2D, is a rolling upland with a local relief of 200 to 300 feet. Less than 25 per cent of the land is in slopes steeper than 14 per cent and the percentage in slopes steeper than 5 per cent varies widely from less than 25 to mor than 75 per cent. Weak, non-cherty dolomite, rock type 4, overlies the resistant cherty dolomitic sandstone of rock type 3 which is exposed only in the valley bottoms. Although the dolomite erodes readily, it is not extensively dissected, because of its location remote from deeply incised drainage lines and because of the presence of the resistant strata in the valleys. The typical swells are two and one half miles wide at the base, presenting a marked contrast to the sharp ridges of the Osage-Gasconade-Meramec River Hills Forest Region.

The residuum on rock type 4 is fine-textured; in level areas it is deep, whereas on slopes it is shallow due to rapid erosion. On summits the sponge-like action of the soil results in a high but fluctuating water table. In depressions extending down the hillsides, also, there usually is adequate soil moisture, but elsewhere on the slopes recurrent deficiency is the rule.

On the summits and in the region as a whole, post oak, red oak and black oak *(Q. velutina)* predominate, but on slopes post oak, black-jack oak and black oak constitute more than 50 per cent of the stand. Here, too, red oak is abundant, being concentrated especially in the moister sites. Cedar *(Juniperus virginiana)* is scattered throughout the region, becoming an important forest element only in the southwestern part. Locally, where the soil is extremely shallow, *glades* or *bald knobs* occur, the latter on hilltops. In these areas small cedars are virtually the only trees and the other plants are chiefly prairie species. Most of the summits of the broad swells have been cleared for agriculture, but because of low soil fertility, much of this land is now being allowed to revert to forest. The slopes and narrow ridge tops are generally forested with timber which is small due partly to unfavorable growth conditions and partly to repeated cutting.

Some zinc deposits, of no present economic importance, occur within the limits of the region, in north-central Arkansas.

The Cleared River Border Region, Figs. 1 and 3A, B, and C, includes the flood plain and terraces[15] of the Missouri and Mississippi rivers, the adjoining breaks, and the rolling, loess-covered upland south of the Missouri and west of the Mississippi. Within this region bed rock is less important as a factor in landscape development than it is in the other parts of the Province. Alluvium covers the bed rock in the lowlands and loess mantles it on the uplands. Hence, the bed rock types find expression only in the river bluffs and in valleys which penetrate the loess to the underlying strata. In general, the influence of the loess decreases from west to east along the Missouri River

15 Percival Robertson, Some Problems of the Middle Mississipi River Region During Pleistocene Time, *Trans. Acad. Sci. of St. Louis* **29**(6), July, 1938.

and then southward along the Mississippi. At the western end of the region, Fig. 3A, a continuous mantle of loess, low differential resistance of the bed rock, rock type 7, and moderate elevation above the Missouri River, result in local relief of 200 to 300 feet and in low angles of slope. Less than 25 per cent of the land is in slopes steeper than 14 per cent, and only 25 to 50 per cent is in slopes steeper than 5 per cent. The average swell is 2.7 miles wide at the base. Farther east along the Missouri River and also in that part of the region bordering the Mississippi 10 to 50 miles south of St. Louis, Fig. 3B, higher elevation above these rivers has resulted in more pronounced erosion

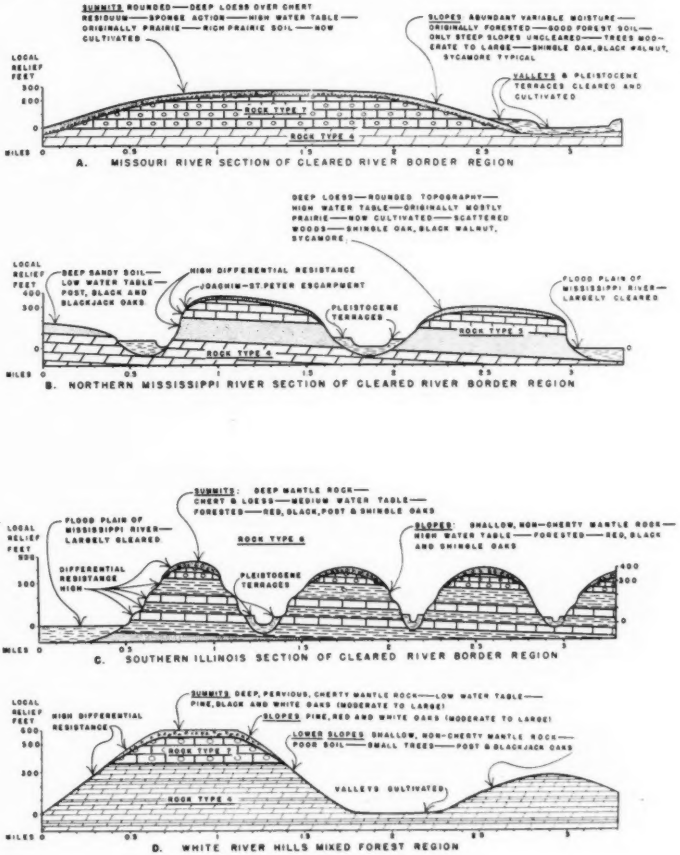
A. MISSOURI RIVER SECTION OF CLEARED RIVER BORDER REGION
B. NORTHERN MISSISSIPPI RIVER SECTION OF CLEARED RIVER BORDER REGION
C. SOUTHERN ILLINOIS SECTION OF CLEARED RIVER BORDER REGION
D. WHITE RIVER HILLS MIXED FOREST REGION

Fig. 3. Physical Profiles II.

and in the exposure, in the valleys, of bed rock of moderate to high differential resistance, rock types 4 and 5. Here, the local relief is 200 to 400 feet and ridges average a mile in width. From 25 to 75 per cent of the land is in slopes steeper than 14 per cent, and from 50 to 100 per cent is in slopes steeper than 5 per cent. Still farther south, in Illinois and adjacent Missouri, Fig. 3C, advanced erosion by minor streams has exposed thin strata of high differential resistance, rock type 6. The rounded, loess-covered summits are narrow; the local relief is 300 to 500 feet; ridges are only .7 mile wide; and steep slopes are common. Here, from 50 to 100 per cent of the land is in slopes steeper than 14 per cent, and from 75 to 100 per cent is in slopes steeper than 5 per cent.

On the broad, loess-covered summits of the swells throughout the Cleared River Border Region the water table is high, a fact which has led to the development of a prairie flora and prairie soils. On the slopes the water table fluctuates, but seepage from the summits is adequate to support moderate to large trees, with shingle oak *(Q. imbricaria)*, black walnut *(Juglans nigra)* and sycamore abundant. The occurrence of small willows along hillside drainage lines near the summits of the swells is characteristic of the region. Most of the area is now under cultivation, except the steeper slopes, the swampy parts of the major flood plains and occasional wood lots at the edges of the uplands.

No minerals of great economic importance are present in the region. The St. Peter sandstone, however, is worked for glass sand, and two of the limestone formations yield high calcium lime.

The White River Hills Mixed Forest Region, Figs. 1 and 3D, displays striking internal contrasts. On the higher ridges caps of massive cherty limestone, rock type 7 (+), protect the underlying non-cherty dolomite, rock type 4 (—), from erosion. The limestone, in turn, is capped by an extremely resistant mantle of its own residual chert. Because of the high differential resistance and the proximity to the deeply intrenched White River, the local relief is 500 to 600 feet and steep land slopes are typical. In most parts of the region more than 50 per cent of the area is in slopes steeper than 14 per cent, and from 75 to 100 per cent is in slopes steeper than 5 per cent. At the base the average ridge is from one and one half to two miles wide.

The chert residuum on the higher hills is deep and pervious; consequently, the water table is low on the summits and fluctuating on the slopes. The soil developed on this mantle, however, is relatively fertile and does not erode severely, even upon steep slopes. In these latter situations the loss of the surface soil exposes chert fragments which effectively retard the removal of the remaining fine material. This surface concentration of rock fragments may be termed a *slope wash pavement*. The forests on the cherty limestone of these higher hills consists of moderate to large trees. On the summits pine, black and white oaks predominate, whereas on the clopes pine, red and white oaks hold the corresponding rank. Even on the summits red oak is abundant, being most numerous where the configuration of surfaace or bed rock concentrates the moisture. Pine and white oak are represented equally in the percentages

for summits and for slopes, but the pines are larger in the former sites.

On the lower flanks of the ridges the dolomite, rock type 4, yields non-cherty mantle rock which erodes readily, leaving a shallow layer to support a scattered growth of small trees. Here, cedar and post oak predominate on the steeper sites and post oak, cedar and black jack oak on those less steep. Glades and bald knobs are numerous. The tops of these low ridges of rock type 4 have deep mantle rock with a little residual chert. The average size of the timber has been reduced by cutting, but the few remaining virgin stands consist of large trees, post, red and black oaks predominating. Within the region cedar is an excellent indicator of rock type 4 and pine of rock type 7. Neither species transgresses the common lithic boundary more than a few feet.

No minerals of economic importance occur in the White River Hills Mixed Forest Region.

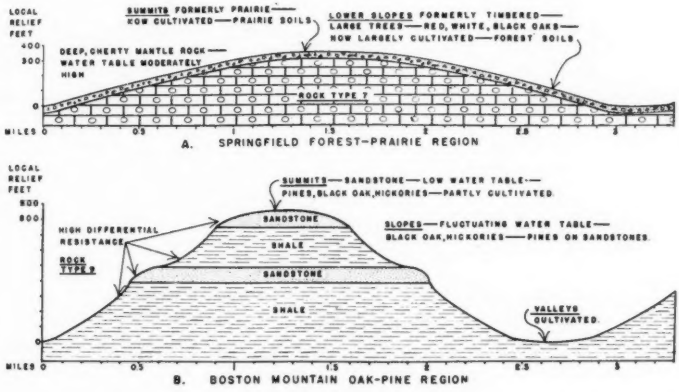

Fig. 4. Physical Profiles III.

The Springfield Forest Prairie Regigon, Figs. 1 and 4A, closely resembles the adjoining western part of the Cleared River Border Region, Fig. 3A, from which it differs principally in its markedly thinner loess mantle. Because the streams, here, unlike those of the White River Hills Mixed Forest Region, have not penetrated the cherty limestone, rock type 7, differential resistance and land slopes are low. In most of the area less than 25 per cent of the land is in slopes steeper than 14 per cent and only in the eastern part does this value exceed 50 per cent. In the northwest less than 25 per cent of the land is in slopes steeper than 5 per cent, but this percentage increases to the southeast and exceeds 75 per cent adjacent to the White River Hills Mixed Forest Region. The swells average three miles in width and the local relief is 300 to 400 feet.

A deep layer of cherty residuum covers the entire area; on level uplands it

is topped by a thin veneer of loess, but on steeper areas slope wash pavements have developed. On the broad summits the water table is high and the native vegetation was, in the past, prairie. Now, however, the rich prairie soils are almost entirely under cultivation. On the hill slopes the deep mantle rock and good soil have led to the growth of a forest of large trees in which the superior timber species, red, white and black oaks, predominate. Pine is virtually absent, here, although abundant on the narrow, well drained caps of the same rock in the White River Hills Mixed Forest Region. Much of the forest has been clared for the cultivation of the relatively fertile, erosion-resisting forest soils.

Within this region are the rich zinc-lead deposits of the Tri-State District of Missouri, Kansas and Oklahoma.

The Boston Mountain Oak-Pine Region, Figs. 1A and 4B, differs from the remainder of the Ozarks in its non-cherty sandstones and shales, rock type 9, which contrast with the cherty dolomites and limestones of the other regions. High differential resistance between the sandstones and limestones (+) on the one hand and the shales (—) on the other, together with strong relief above bordering areas, has resulted in the development of high ridges with rounded summits and valleys of moderate width. Resistant sandstones cap the hills and shales erode to form the valleys. On the hillsides the alternation of sandstones and a few thin limestones (+) with shales (—) results in a succession of convex and concave slopes. The ridges are two and one half miles wide at the base, and the local relief commonly is between 800 and 900 feet. From 50 to 75 per cent of the land is in slopes steeper than 14 per cent, and more than 75 per cent is in slopes steeper than 5 per cent.

Due to the absence of chert, erosion is active and mantle rock is thin, except on the broader hilltops. The sandstone-capped summits have sandy soils, low water tables, and support a forest of which pine, black oak and hickories are outstanding constituents. On the slopes soil moisture is at times deficient and the tree species are much the same as those on the summits. Formerly, the forest consisted of medium-sized trees, but cutting has removed much of the larger timber in the more accessible locations. The valleys and many of the broader ridge-tops are now cultivated.

To the present time no mineral deposits of economic importance have been discovered in the region.

Appendix

During the field and library investigations undertaken in the preparation of this paper, geological information was accumulated and organized to form a background for studies in Ozark geography and ecology. As this material is not generally available, it was considered desirable to summarize it in the generalized rock column, Fig. 5, and the accompanying description. The geological material here presented exhibits several aspects of novelty. First, the rocks are differentiated into types according to their regional lithologic character which is expressed in landform development, soils and native vegetation; geologic age is mentioned chiefly to facilitate reference to the literature.

Second, the resistance of the various rocks to weathering and erosion is represented by a bar graph attached to the right side of the rock column. And third, the column is interrupted to show those mantle rocks which are important elements in the regional complexes. Each rock type includes only strata or igneous masses which are associated areally and which collectively function as a unit in landscape development. Following this principle, Ordovician and Mississippian strata, which occur in one region in unconformable contact, are grouped as rock type 5, and the Silurian and Devonian beds, which, in a conventional rock column, would appear between them, are classed as rock type 6 because they are found only in another part of the Province where they exhibit elements of regional unity. Some of the types include dissimilar strata, the combination and not the individual members being characteristic.

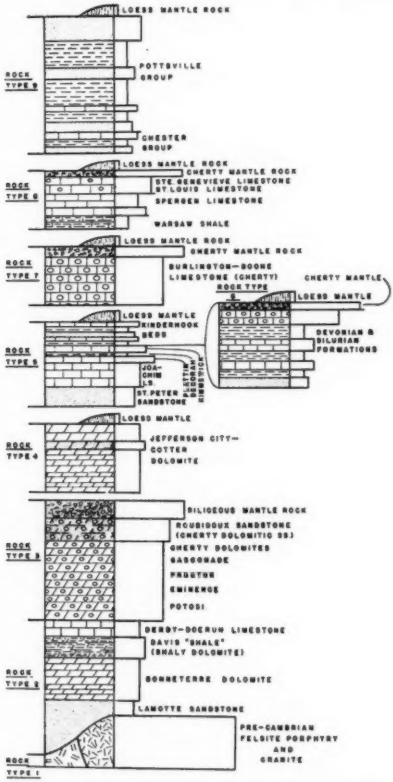

Fig. 5. Generalized Rock Column for the Ozark Province (showing order of superposition of functional rock types and differential resistance among individual units).

The following description will emphasize the essential characteristics of the various rock types:

Type 9, Description:

Bed rock—*thick shales interbedded with thinner strata of sandstone and a little limestone.*

Geologic age—Mississippian and lower Pennsylvanian (Chester and Pottsville).

Mantle rock—loess, residual clays and sands.

Permeability—low in shale; high in sandstone; variable in mantle rock.

Individual resistances[16]—low.

Differential resistance—moderate to high (sandstones and limestones (+), shales (—)).

Type 8, Description:

Bed rock—*moderately cherty and non-cherty limestones and calcareous shales.*

Geologic age—Mississippian (Warsaw through Ste. Genevieve).

Mantle rock—variable; loess on hilltops, thin chert on cherty limestones, clay on shales and non-cherty limestones.

Permeability—generally low in bed rock; high in mantle rock, except in clays.

Subsurface drainage—well developed through sinks and limestone caverns.

Individual resistance—low to moderate.

Differential resistance—high between limestone (+) and shale (—).

Type 7, Description:

Bed rock—*thick-bedded, highly cherty limestone.*

Geologic age—lower Mississippian (Burlington-Boone).

Mantle rock—thick, cherty; loess veneer on level uplands.

Permeability—generally moderate; high in mantle rock.

Subsurface drainage—well developed through sinks and caverns.

Underdrainage—pronounced through mantle rock in valleys.

Individual resistances—moderate.

Differential resisttance—low among strata; high between cherty mantle rock (+) and bed rock (—).

Type 6, Description:

Bed rock—*thin shales, limestones and sandstones, capped by cherty limestone.*

Geologic age—Silurian and Devonian.

Mantle rock—moderately thick, cherty in places; loess on hilltops.

Permeability—generally low and variable among strata.

Individual resistances—low to moderate.

Differential resistance—high between shales (—) and other strata (+) and between cherty mantle rock (+) and underlying beds (—).

Type 5, Description:

Bed rock—*non-cherty sandstones, limestones and shales; upper formations thin, lower thicker.*

Geologic age—middle Ordovician and lower Mississippian (St. Peter through Kinderhook).

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16 Individual resistance is the qualitative expression of the ability of any uniform rock mass to withstand weathering and erosion. This term is substituted for "absolute resistance," previously used.[17]

17 Cozzens, op. cit. p. 45.

Mantle rock—non-cherty clays and sands.
Permeability—variable among upper strata; high in thick St. Peter sandstone at base.
Individual resistances—low to moderate.
Differential resistance—high between adjoining formations and strata.

Type 4, Description:
Bed rock—*relatively non-cherty, fine-grained dolomite.*
Geologic age—middle Ordovician (Jefferson City-Cotter).
Mantle rock—extremely thin (less than 6 inches on slopes).
Permeability—high near surface through closely spaced joints and bedding planes.
Individual resistances—moderate.
Differential resistance—moderate.

Type 3, Description:
Bed rock—*highly cherty, coarse-grained dolomite overlaid by cherty, dolomitic sandstone.*
Geologic age—Cambrian and lower Ordovician (Potosi through Roubidoux).
Mantle rock—extremely deep siliceous (quartz druse, chert and quartzite).
Permeability—mantle rock very high; bed rock generally moderate.
Subsurface drainage—well developed through mantle rock and through sinks and caverns.
Underdrainage—much through mantle rock in valleys.
Individual resistances—high above, moderate below.
Differential resistance—moderate to high between sandstone (+) and dolomite (—); high between heavy siliceous residuum (+) and bed rock (—).

Type 2, Description:
Bed rock—*non-cherty sandstone, dolomite, shaly dolomite and limestone.*
Geologic age—upper Cambrian (Lamotte through Derby-Doerun).
Mantle rock—deep sands and clays.
Permeability—variable; high in Lamotte sandstone at base.
Subsurface drainage—slightly developed through sinks.
Individual resistances—low to moderate, generally decreasing downward.
Differential resistance—moderate; most strata (+) with respect to underlying beds (—).
Economic minerals—important deposits of disseminated galena.

Type 1, Description:
Bed rock—*granite and felsite porphyry.*
Geologic age—pre-Cambrian.
Mantle rock—shallow clay; some arkosic sand.
Permeability—extremely low (penetration limited to widely spaced joints).
Individual resistances—very high.
Differential resistance—low.
Economic minerals—specular hematite (formerly important locally).

SECTION OF GEOGRAPHY,
UNIVERSITY OF ILLINOIS,
URBANA, ILL.

An Annotated Bibliography of Arkansas Ornithology

William H. Deaderick

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———1831-1839—Ornithological Biography. Five vols. Philadelphia.—Contains records of several birds observed in Arkansas including the Alder Flycatcher, Snowy Owl, White-fronted and Canada Geese, Long-billed Curlew, Bonaparte Gull, American Merganser and Trumpeter Swan.

BACON, W. J. 1907—A Camp Hunt in Arkansas. Amer. Field **67**:362.—Mentions wild turkeys near Clarendon.

BAER, G. WILLIAM J. 1926—Trying to Tame a Great Horned Owl. Auk **43**:214.

———1927—Summer Birds of Mount Magazine, Logan County, Arkansas. Auk **44**:545.

———1930a—The Song Period of Birds of Northwest Arkansas. Auk **47**:32.—Song records of 76 species from 1924 to 1928.

———1930b—Bird Migration Records in Northwest Arkansas. Wilson Bull. **42**:44.—Migration dates of 81 species from 1924 to 1928.

———1930c—Starling in Arkansas. Auk **47**:256.—One collected on the university campus, the first record for the state.

———1931—Birds of Arkansas. Fayetteville. 1-197.—An account of 312 species, 297 of which have been reported from Arkansas, 15 included on good circumstantial evidence.

———1933—Record of the Starling in Arkansas: a Correction. Wilson Bull. **45**:29.—Corrects the statement of Black 1932b.

———1937—Elementary Ornithology. Mimeographed.—A manual of 62 pages for the author's classes in the University of Arkansas.

BAIRD, BREWER AND RIDGWAY. 1874—A History of North American Birds. Land Birds, Boston.—Records of the Paroquet, Yellow-breasted Chat, Redstart, Traill's Flycatcher and Ivory-billed Woodpecker.

BAIRD, CASSIN AND LAWRENCE. 1858—Exploration for a Railroad Route from the Mississippi River to the Pacific, **9**. Washington.—A Carolina Paroquet is reported from near Fort Smith.

BARROWS, WALTER B. 1889—The English Sparrow (Passer domesticus) in North America. U. S. Dept. Agric., Div. Econ. Ornith. and Mamm. **1**:1-405.—Contains record of first importation into Arkansas and notes on habits in the state.

BARTSCH, PAUL. 1917—Destruction of Passenger Pigeons in Arkansas. Auk **34**:87.—Describes the destruction of a pigeon roost near Hickory Plains, White County, around the year 1879.

BENDIRE, CHARLES. 1892-1896—Life Histories of North American Birds. 2 volumes, Washington.—Contains numerous reports from Arkansas including the only record of the Duck Hawk from this state.

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———1921—Life Histories of North American Gulls and Terns. Bull. U. S. Nat. Museum **113**.

———1922—Life Histories of North American Petrels, Pelicans and their Allies. Bull. U. S. Nat. Museum **121**.

———1923—Life Histories of North American Wildfowl, part 1. Bull. U. S. Nat. Museum **126**.

———1925—Life Histories of North American Wildfowl, part 2. Bull. U. S. Nat. Museum **130**.

———1927—Life Histories of North American Marsh Birds. Bull. U. S. Nat. Museum **135**.

———1927—Life Histories of North American Shore Birds, part 1. Bull. U. S. Nat. Museum **142**.

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———1932—Life Histories of North American Gallinaceous Birds. Bull. U. S. Nat. Museum **162**.

———1937—Life Histories of North American Birds of Prey, part 1. Bull. U. S. Nat. Museum **167**.

———1938—Life Histories of North American Birds of Prey, part 2. Bull. U. S. Nat. Museum **170**.

———1939—Life Histories of North American Woodpeckers. Bull. U. S. Nat. Museum **174**.—Numerous Arkansas records are included. The local value of these volumes consists of distributional and migratory data.

BLACK, J. D. 1925—The Blue-headed Vireo. Oologist **42**:120.—Observed as a spring migrant at Winslow.

———1928—The Sycamore Warbler in Arkansas. Wilson Bull. **40**:251.—Adults observed feeding young near Winslow.

———1929a—The Bald Eagle in Arkansas. Wilson Bull. **41**:41.—An adult observed at Winslow.

———1929a—Nesting of the Purple Finch in Arkansas. Wilson Bull. **41**:190.—A small colony reported nesting in cedar trees one mile south of Winslow.

———1931—Pectoral Sandpiper at Winslow. Wilson Bull. **43**:223.—A specimen collected near Winslow May 12, 1931.

———1932a—A Winter Robin Roost in Arkansas. Wilson Bull. **44**:13.—A roost near Winslow is described, containing, at one time, over 250,000 birds.

———1932b—The Record of the Starling in Arkansas. Wilson Bull. **44**:235.—Disputes Baerg's (1930c) priority in recording the Starling in Arkansas.

———1932c—The Bohemian Waxwing in Arkansas. Wilson Bull. **44**:240.—A flock of 10 observed near Winslow (?) May 12, 1931.

———1933a—Snowy Egret in Arkansas. Auk **50**:206.—Reports the skeleton of a specimen which was identified by Dr. Alexander Wetmore.

———1933b—Long-eared and Short-eared Owls in Akansas. Auk **50**:436.—A specimen of each is recorded from the Fayetteville area.

———1935a—Birds of the Winslow, Arkansas Region. Amer. Midl. Nat. **16**:154.—An annotated list of 175 species.

———1935b—The Southern Crow in Arkansas. Auk **52**:90.—Reports a specimen shot near Fort Smith.

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BOWDEN, GEORGE W. C. 1902—A Duck Hunt in Arkansas. Amer. Field **57**:166.—Mentions ducks and coots in Crawford County.

BREWSTER, WILLIAM. 1902—An Undescribed Form of the Black Duck (Anas obscura).—Records a specimen in the Museum of Comparative Zoology collected in Mississippi County.

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Maj. Townsend of specimens of Icterus xanthocephalus and Recurvirostra americana from Arkansas, the only records of either species from this state.

CAVANESS, SALLIE. 1911—Bird-Lore's Eleventh Bird Census. Bird-Lore **13**:41.—Reports 19 species observed at Monticello.

CHAFIN, BEEBE THOMPSON. 1923—Our Winter Guests. Bird-Lore **25**:375.—Account of common winter birds at Monticello.

CHAPIN, MRS. J. T. AND SALLIE AND VIRGIE CAVANESS. 1923—Christmas Bird Census Bird-Lore **25**:39.—Report 30 species observed at Monticello.

CHAPMAN, FRANK M. 1914—The Warblers of North America. New York 1-306.—Contains records of eight species from Helena.

COOKE, WELLS WOODBRIDGE. 1883—Mississippi Valley Migration. Orn. and Ool. **8**:33.—Records a number of birds observed at Fayetteville by Prof. F. L. Harvey.

———1888—Report on Bird Migration in the Mississippi Valley in the Years 1884 and 1885. U. S. Dept. Agric., Div. Econ. Ornith. **2**:213.—Contains numerous records from Arkansas including the Ruffed Grouse, Ivory-billed and Red-cockaded Woodpeckers, Smith's and Lapland Longspurs, Sprague's Titlark, and the Brownheaded Nuthatch.

———1903-1906—The Migration of Warblers. Bird-Lore **5**:189; **6**:22; **7**:33; 135, 203, 278; **8**:168.—Contains numerous Arkansas records.

———1904—Distribution and Migration of North American Warblers. Biol. Surv. Bull. **18**, Washington.—Contains numerous records from Arkansas.

———1907—The Migration of Thrushes. Bird-Lore **9**:32.—Contains records from Helena.

———1907-1909—The Migration of Flycatchers. Bird-Lore **10**:115; **11**:12.—Contains records from Helena.

———1909—The Migration of Vireos. Bird-Lore **11**:79, 116, 118.—Contains records from Helena.

———1909-1914—The Migration of North American Sparrows. Bird-Lore **11**:257; **12**:15; **13**:15, 200, 249; **14**:45, 98, 103, 160, 288; **15**:107; **16**:440.—Contains numerous Arkansas records.

———1910—Distribution and Migration of North American Shore Birds. U. S. Dept. Agric., Biol. Surv. Bull. **35**, Washington.—Contains records of Golden plover seen at Fayetteville.

———1915a—The Migration of North American Kinglets. Bird-Lore **17**:118.—Contains records from Helena and from central Arkansas.

———1915b—The Migration of North American Birds; Brown Creeper and Gnatcatchers. Bird-Lore **17**:199.—Contains records from Clinton, Delight and Helena.

———1915c—The Migration of North American Birds; The Nuthatches. Bird-Lore **17**:443.—Contains a record of the Red-breasted Nuthatch at Helena.

CRAMER, ZADOK. 1821—The Navigator. 11th ed., Pittsburgh. Writing of Porter's Lake, just north of Helena, mentions swans, geese and ducks.

CROOKS, F. D. 1939—Starlings nesting near Rogers, Arkansas. Auk **56**:477.—Reports the finding of three nests and the observation of numerous young.

COUES, ELLIOTT. 1879—Southward Range of Centrophanes lapponica. Bull. Nutt. Orn. Club **4**:238.—Records of Lapland Longspur and Sprague's Pipit in Arkansas.

DEADERICK, WILLIAM H. 1935—Some Notes from Arkansas. Auk **53**:324.—Records of the Red-throated Loon, Common and Caspian Terns, Pectoral Sandpiper, White-rumped Sandpiper, Semipalmated Sandpiper, Philadelphia Vireo, Red-breasted Nuthatch, Blackburnian Warbler and Black-poll Warbler.

———1936a—Some Notes from Arkansas. Auk **53**:349.—Records of the Common Loon, Horned Grebe, White Pelican, Buffle-head, Red-breasted Merganser,

Southern Bald Eagle, Osprey, Greater and Lesser Yellow-legs, Blue-headed Vireo and Orange-crowned Warbler.

———1936b—Some Notes from Arkansas. Auk **53**:455.—Records of the Baldpate, King Rail, Golden Plover, Western House Wren, Connecticut and Wilson's Warblers, Northern Pine Siskin and Dakota Song Sparrow.

———1937—The Willet in Arkansas. Auk **54**:207.—Correcting an error of identification of Western Willet reported (1936b) as Eastern Willet.

———1939—A Preliminary List of the Birds of Hot Springs National Park and Vicinity. Wilson Bulletin **50**:257.—An annotated list of 208 species, 14 of which are additions to the state list, observed in Garland County.

DEANE, RUTHVEN. 1895—Additional Records of the Passenger Pigeon in Illinois and Indiana. Auk **12**:298.—Mentions wild pigeons taken at Siloam Springs.

DUMONT, PHILIP A. 1933—An Old Specimen of Hybrid Flicker from Central Arkansas. Auk **50**:362.—Concerns a hybrid between *Colaptes auratus* and *C. cafer*, taken in Faulkner County, March 26, 1882.

DUNBAR, WILLIAM. 1804—Journal of a Voyage. From "Life, Letters and Papers of William Dunbar, Jackson, Miss."—Numerous records of swans, ducks, geese, and turkeys.

DU PRATZ, ANTOINEE SIMON LE PAGE. 1758—History of Louisiana. English translation, London, 1763. From the territory which became Arkansas he records pheasants, partridges, snipe and woodcock. It is probable that some of the 59 species in his annotated list from "Louisiana" were observed in Arkansas.

FEATHERSTONAUGH, GEORGE WILLIAM. 1840—Excursion Through the Slave States. 2 vols. London.—Observed an Ivory-billed Woodpecker in northeast Arkansas.

FLINT, TIMOTHY. 1826—Recollections of the Last Ten Years Passed in Occasional Residences and Journeyings in the Valley of the Mississippi. Boston.—On a visit to Arkansas in 1819 he records the Blue Jay, the first report of this species in the state.

GAULT, BENJAMIN T. 1896—Some Bluebird Notes. Nidiologist **3**:84.—Mentions Bluebirds near Paragould.

GREGG, H. R. 1935—White-throated Swift at Hot Springs Natiional Park, Arkansas. Auk **52**:452.—One collected May 4, 1935, in an office building.

GERSTAECKER, FREDERICK. 1839-1842—Wild Sports in the Far West. New York, n.d. —Reports numerous turkeys, ducks, wild geese and tells of shooting an eagle.

"GRÖMBECK." 1890—Arkansas Wild Turkeys. Forest and Stream **34**:169.—Records of Wild Turkeys and Quail from Arkadelphia.

HARVEY, F. L. 1880—Voraciousness of Chordeiles popetue Baird. Amer. Nat. **14**:896. —Records taking over 600 insects from one stomach.

———1882—Habits of the Woodcock. Amer. Nat. **16**:737.

HASBROUCK, EDWIN M. 1891a—The Present Status of the Ivory-billed Woodpecker (Campephilus principalis). Auk **8**:174.—Reported still abundant at Newport in 1885.

———1891b—The Carolina Paroquet (Conurus carolensis). Auk **8**:369.—Mentions only one record for Arkansas, that by Baird, Brewer and Ridgeway in 1874 who speak of its occurrence in considerable numbers.

HAY, OLIVER P. 1882—A List of Birds from the Lower Mississippi Valley Observed during the Summer of 1881, with Brief Notes. Bull. Nutt. Orn. Club **7**:89.—Contains notes on 29 species observed near Hopefield.

HOLLISTER, NED. 1902—Notes on the Winter Birds of Arkansas. Wilson Bull. **9**:10.—An annotated list of 51 species observed on Grand and White River Prairies.

HOWELL, ARTHUR HOLMES. 1911—Birds of Arkansas. Biol. Surv. Bull. **38**, Washington.—An annotated list of 255 species and subspecies.

HUNT, CHRESWELL J. 1920—Sunlight and Shadow. Condor **22**:186.—Records the Black-throated Green Warbler in Arkansas.

———1921a—Notes of the Winter and Early Spring Birds of Southeastern Arkansas. Auk **38**:370.—Notes on about 98 species observed near Tillar.

———1921b—Additional Notes on Arkansas Birds. Auk **38**:610.—Treats of several species observed at Chicot.

———1931—Notes on the Winter Birds of Arkansas. Auk **48**:235.—An annotated list of 73 species observed in Pulaski and surrounding counties.

JAY, CLELL. 1935—Eureka Springs, Ark., 1935 Data. Oologist **52**:68. Brief data, mostly nesting, of 35 species.

JOUTEL, HENRY. 1687—Historical Journal of M. de LaSalle's Last Voyage to Discover the River Mississippi. From French's Historical Collections of Louisiana, New York, 1846.—Record of "turkeys, bustards, swans, teal and other game" at Arkansas Post.

KENNERLY, CALEB B. R. 1859—Route Near the Thirty-fifth Parallel Explored by Lieut. Whipple. Pacific R. R. Report 10, part 6, no. 3.—Contains records of Carolina Paroquet and Yellow-crowned Night Heron from Fort Smith.

LA HARPE, BERNARD DE. 1721-1722—La Harpe's Expedition on the Arkansas. From "Along the Arkansas" by Anna Lewis, Dallas, 1932.—He found turkeys plentiful, some of which he killed.

LANO, ALBERT. 1913—Greater Snow Goose in Arkansas. Auk **30**:579. One collected March. 28, 1913, near Fayetteville.

———1921a—Prairie Chicken (Tympanuchus americanus) in Arkansas. Auk **38**:112.

———1921b—American Osprey in Arkansas. Auk **38**:113.—One collected near Fayetteville, Sept. 20, 1919.

———1926a—Ring-billed Gull in Arkansas. Auk **43**:87.—One collected near Fayetteville, Sept. 27, 1919.

———1926b—Krider's Hawk in Arkansas. Auk **43**:368.—A specimen collected near Fayetteville was identified by Dr. Oberholser.

———1927—Great Blue Heron Electrocuted. Auk **44**:246.—A dead specimen picked up beneath several high power electric light wires.

LATROBE, CHARLES JOSEPH. 1836—The Rambler in North America. 2 vols., London.—Vol. I mentions swans, turkeys and wild pigeons.

MARQUETTE, JAQUES AND LOUIS JOLIET. 1673—An account of the Discovery of Some New Countries and Nations in North America in 1673. In Historical Collections of Louisiana, Compiled by B. F. French, part 2, Phila., 1850.—Near what is supposed to be the site of the present town of Helena they "saw quails and shot a parrot which had half of his head red, the neck yellow, and the rest of the body green."

MCATEE, WALDO LEE. 1911—Local Names of Waterfowl and Other Birds. Forest and Stream **77**:172.—Contains numerous records of the commoner birds of Arkansas.

———1923—Ducks Useful in Arkansas as Scavengers of Red Rice. Auk **40**:527.—Directions for harvesting, care of land and protection of ducks.

———1931—Local Names of Migratory Game Birds. U. S. Dept. Agric. Misc. Circ. **13**, Washington.—Contains numerous records of the more common birds.

MERRILL, D. E. 1934—Starling in Benton County, Arkansas. Auk **52**:191.—Eight observed Jan. 10, 1934, and five at later dates.

MITCHELL, ROBERT H. 1894—Capture of Clarke's Nutcracker in Crittenden County, Arkansas. Auk **11**:327.—Records one killed at Earle about April 1, 1891.

MORPHEW, L. R. 1907—Arkansas Birds. Forest and Stream **68**:536.—Mentions wild pigeons and other birds seen near Hot Springs.

NATIONAL PARK SERVICE. 1937—Check List of the Birds of the National Parks. Mime-

ographed, Washington.—Contains an annotated list of the birds of Hot Springs National Park and vicinity.

NUTTALL, THOMAS. 1821—A Journal of Travels into the Arkansas Territory, 1819. Vol. 13 of Thwaite's Early Western Travels, Cleveland, 1905.—Mentions flocks of screaming parrots, wild geese, Whip-poor-will, Mockingbird, Cardinal, Bluebird and Bald Eagle, a small list for one who later wrote the leading ornithological handbook of his time.

———1832—A Manual of the Ornithology of the United States and Canada. The Land Birds, Cambridge.—Mentions the Whip-poor-will, Bluebird and Carolina Paroquet in Arkansas.

OBERHOLZER, HARRY CHURCH. 1917—Critical Notes on the Eastern Subspecies of Sitta Carolinensis Latham. Auk **34**:181.—A record from Van Buren.

———1918a—The Migration of North American Birds. The Scarlet and Louisiana Tanagers. Bird-Lore **20**:145.—Contains records from Helena.

———1918c—The Migration of North American Birds. The Waxwings and Phainopepla. Bird-Lore **20**:219.—Contains records from Helena.

———1920—The Migrations of North American Birds. Cowbirds. Bird-Lore **22**:343.—Contains records from Delight.

———1921—The Geographic Races of Cyanocitta Cristata. Auk **38**:83.—A record from Delight.

———1922—The Migration of North American Birds. Baltimore Oriole. Bird-Lore **24**:338.—Contains records from Helena.

———1923—The Migration of North American Birds. Orchard Oriole. Bird-Lore **25**:119.—Contains records from Helena.

"OLD-TIMER." 1899—Duck Hunting in Arkansas. Amer. Field **52**:181.—Mentions several species seen near Alma.

OWENS, CHARLES M. 1935—Bay-breasted Warbler in Arkansas. Auk **52**, 414.—One observed, apparently the first recorded in the state, near Monticello.

PINDAR, L. OTLEY. 1924—Winter Birds in Eastern Arkansas. Wilson Bull. **36**:201.—Notes on 114 species observed at Helena and at Marked Tree during the Winter of 1888-1889. Contains the sole records of several species for the state, including Holboell's Grebe, American Eared Grebe and Whistling Swan.

PLANK, W. 1911—Notes on the Olive-sided Flycatcher. Oologist **28**:154.—Observed at Decatur.

PLEAS, C. E. 1888—Van Buren County, Arkansas, Notes. Oologist **5**:124.

———1889—Arkansas Notes. Oologist **6**:130.—Numerous records from Clinton.

———1890a—Chuck-Will's-widow at Clinton, Arkansas. Ooologist **7**:142.

———1890b—The Caprimulgidae in Arkansas. Oologist **7**:155.—Habits of three species at Clinton.

———1890c—Fairies in a Fairyland. Oologist **7**:215.—Ruby-throated hummingbird at Clinton.

———1892b—Some of Our Visitors and Neighbors. Oologist **9**:160.—Habits of the Ruby-throated Hummingbird at Clinton.

———1895—From a Rusty Pen. Oologist **12**:155.—Notes on several species at Clinton.

———1896—The Story of a Find. Oologist **13**:34.—Records the nesting of Bewick's Wren at Clinton.

———1897—Carolina Rail at a High Elevation. Osprey **1**:67.—Records one killed on Pinnacle Mountain near Clinton.

PLEAS, LILLIE. 1891a—Feeding the Birds in Winter. Oologist **8**:156.—Notes on various species at Clinton.

———1891b—The Screech Owl. Oologist **8**:195.—Habits at Clinton.

———1891c—The Great Carolina Wren. Oologist **8**:215.—Habits at Clinton.

———1891d—The Pileated Woodpecker. Oologist **8**:236.—Habits at Clinton.

———1891e—The Blue-gray Gnatcatcher. Oologist **8**:239.

———1891e—The Blue-gray Gnatcatcher. Oologist **8**:239.

———1892—Our Winter Visitors. Oologist **9**:44.—Notes on various species at Clinton.

———1897—A Baby Ruby-throated Hummingbird. Osprey **1**:136.—Habits at Clinton.

RAGSDALE, GEORGE HENRY. 1889—On the Hiatus Existing Between the breeding Ranges of the Loggerhead and White-rumped Shrikes. Auk **6**:224.—Records of the Loggerhead Shrike in Arkansas.

REYNOLDS, H. S. 1877—Winter Birds of Arkansas. Amer. Nat. **11**:307.—Notes on 29 species observed near Judsonia. The first local list in the state. Omits the Cardinal and states that the Summer Tanager "enlivened the landscape all winter."

SCHOOLCRAFT, HENRY ROWE. 1821—Journal of a Tour into the Interior of Missouri and Arkansas. London.—He mentions turkeys, ducks, brant geese, an eagle, a hawk, a heron and a prairie hen.

SMITH, AUSTIN PAUL. 1915—Birds of the Boston Mountains, Arkansas. Condor **17**:41.—An annotated list of 143 species observed near Winslow.

STEPHENSON, LOUISE M. 1895—Why are There so Few Bluebirds? Forest and Stream **45**:150.—Contains numerous Arkansas records.

WETMORE, ALEXANDER. 1912—New Records from Arkansas. Auk **29**:112.—Records of Spinus p. pinus and Dryobates borealis collected near Mena in Dec. 1910.

———1918—Bird-Lore's Christmas Census. Bird-Lore **20**:45.—Records of 40 species seen near DeWitt.

WHEELER, H. E. 1922a—Random Notes from Arkansas. Wilson Bull. **34**:221.—Notes on ten species including the Scissor-tailed Flycatcher.

———1922b—The Fish Crow in Arkansas. Wilson Bull. **34**:239.—Reports sight records from five Arkansas counties.

———1923—Random Notes from Arkansas. Wilson Bull. **35**:35.—Notes on six species including Bachman's Sparrow and the Blue Grosbeak.

———1924—The Birds of Arkansas. Little Rock. 184 pp.—An account of 150 permanent and summer residents.

WIDMANN, OTTO. 1896—Bachman's Warbler in Greene County, Arkansas. Auk **13**:264.—Specimens seen May 7 and 9, 1896.

———1907—A Preliminary Catalogue of the Birds of Missouri. Trans. Acad. Sci. St. Louis **17**: no. 1.—Contains a few records for Arkansas.

———1908—Another Clarke's Crow Taken in Missouri. Auk **25**, 222.—Mentions a specimen taken in Crittenden County, Arkansas.

WIER, D. B. ("BYRNE"). 1881—An Arkansas Game Country. Forest and Stream **17**:430.—Mentions several species, including Sandhill Crane, seen near Crockett's Bluff.

———1882a—Habits of Cormorants. Forest and Stream **18**:27.—Record of Phalacrocorax auritus near Crockett's Bluff.

———1882b—Sport on the "Arkansaw" Prairies. Forest and Stream **19**:386.—Mentions Golden Plover and other birds seen near Crockette's Bluff.

———1882c—On the "Arkansaw" Prairies. Forest and Stream **19**:308.—Records the Whooping Crane seen near Crockett's Bluff.

———1883—The Carrion Crow. Forest and Stream **20**:45.—Habits at Crockett's Bluff.

"YELL." 1880—Albino Robin and Black Opossum. Forest and Stream **14**:44.—An albino robin taken at Jacksonport.

———1885—The Big Woodpecker. Forest and Stream **24**:407.—Record of the Ivory billed Woodpecker at Newport.

HOT SPRINGS, ARK.

Notes and Discussion

A Rapid Method for Recording Angles

H. C. Cutler

The tedious task of measuring and plotting angles of branch and vein divergence has prevented more widespread use of a character which is often a valuable aid in determination of species and in measures of variation. The angle of divergence of branches from the main axis has been of particular value in the genus *Ephedra* (Cutler, 1939) where sterile or staminate material is often difficult to identify. The measurements may be readily made from herbarium material by using those branches which are given off in the plane of the sheet. The table (Fig. 1) gives the angles obtained in a study on *Ephedra* species of North America, as many measurements as possible being taken from each specimen.

Anderson and Ownbey (1939) found that *Nicotiana alata* had an angle of divergence of appendages and branches from the main stem and of side-veins from the midrib of the leaf more acute than in *N. Langsdorffii*. In species of *Acer*, however, the variation within a species is as great as that between them (Anderson and Hubricht, unpublished data) although there are significant differences in the species averages.

	0°-15°	16°-30°	31°-45°	46°-60°	61°-75°	76°-90°	
E. trifurca	3	*42*	40	2			87
E. intermixta		7	*9*				16
E. Torreyana		2	45	*104*	30	3	184
E. arenicola		4	*12*	6			22
E. funerea			8	*16*	18	3	45
E. californica			3	*42*	35	8	88
E. aspera	2	49	*116*	52	8		227
E. fasciculata		12	*27*	10	3		52
E. Clokeyi		4	*62*	21	3		90
E. nevadensis		8	*64*	59	10		141
f. *rosea*			*19*	8	1		28
E. viridis	2	37	*48*	1			88
E. Coryi	8	*45*	13	2			68
var. *viscida*	6	*13*	9				28
E. antisyphilitica			10	*21*	12	2	45
E. compacta		5	*54*	6			65
E. jedunculata		1	3	*11*	3		18

Fig. 1. Table of angles of branch divergence in *Ephedra*.

A device to make such records quickly is shown in Fig. 2. A five inch long blade (A) passes through the slide (B, shown in the inset) mounted three inches from the lower edge of a four by five inch board (C). The blade is pivoted on a hinged arm (D). A card slipped under the edges of the thumbtacks (E) on the baseboard is pricked by the sharpened screw on the blade when the blade is depressed and a record of the angle between the hinged arm and the baseboard is produced. Records of several species and varieties can be kept in parallel lines on the same card and the range of variation and average values determined by inspection.

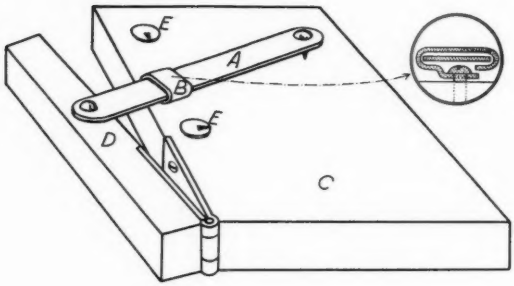

Fig. 2. Explanation in text.

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Book Reviews

THE INVERTEBRATES: PROTOZOA THROUGH CTENOPHORA. By Libbie Henrietta Hyman. McGraw-Hill Book Company, New York, 1940. xii+726 pages. $7.00.

The field of Invertebrate Zoology has outgrown the relatively static condition in which it found itself a generation ago. The journals have been filled with individual researches and programs of new developments but no one has previously attempted to give, in English, an analytic and synthetic covering of this field. For an earlier generation, the Cambridge Natural History and Lankester's Treatise on Zoology reflected the current level of intimate knowledge to supplement the basic materials on morphology and taxonomy in such familiar class room and laboratory texts as Parker and Haswell and the Kingsley-Hertwig in very satisfactory manner.

To the current generation, the continuations of Bronn's Tierreichs gave the only critical evaluation for some of the invertebrate phyla until the Kükenthal Handbuch (1923) came into the field. While these volumes served the advanced front of investigators, who were not excluded from their use because of their being in a foreign language, they were not readily available as reference works for the huge body of zoological students in English speaking countries. Furthermore, the prices at which these sets were sold were prohibitive for inclusion in private libraries and even the individual volumes, representing limited fields of specialization, were too expensive for individual purchase.

A number of years ago, comprehensive works in English began to make their appearance in the United States and in Great Britain but all of these have been confined to restricted areas of the invertebrate field, such as the subjects of Protozoology, Entomology and Parasitology, and still left the field wide open for a comprehensive covering of the realm of the invertebrates. Now, for the first time, a series of treatises is proposed and the initial volume raises high hopes for continuation of the series, for Dr. Hyman has given a masterly analysis of the materials and has shown a familiarity with the literature which few can equal.

The initial volume includes a preview of the entire system of classification of invertebrates, prefaced by a history of the general system of classification in which rather surprising emphasis is placed on the proposals of the older German school of phylogeny and promorphology. "Branches" and "Grades" are introduced as subdivisions of the Subkingdom Metazoa to show how the phyla may be grouped and such terms as "Radiata" and "Bilateria" find a place in the survey of animal groups. Dr. Hyman's position in this regard is clearly expressed in the following quotation (page 32): "The author believes that groupings based upon theoretical considerations such as Protostomia and Deuterostomia should not be regarded as taxonomic divisions but rather as convenient terms for purposes of discussion."

The author seems to have worked under the urge to discard names when later investigators by subdividing a group left it with a more limited inclusion. Thus she proposes Cnidaria as name for the phylum Coelenterata because the more familiar term had originally included likewise the sponges and ctenophores. Though she rationalizes such changes in building her formal categories of taxonomy, she continuously refers to "the coelenterates" in the descriptive portions of the text and (page 365) states, "But the word coelenterates is useful and will be frequently employed." The arbitrary basis for such acceptance or rejection is shown by the fact that in some other instances terms which have become distinctly more limited, than when first proposed, are accepted in a restricted sense. Radiata, under which Cuvier embraced coelenterates and echinoderms is revived and modernized as "Grade I" under the "Branch Eumetazoa" to accommodate the phyla Cnidaria and Ctenophora.

Miss Hyman, perhaps rightly, objects (page 32) to the use of Vermes as a phylum in the Kükenthal-Krumbach Handbuch because this group "can only be defined in

general and mostly negative terms (i.e., as worm-like animals without skeleton or jointed appendages) and which unites animals of remote and indeterminable relationship while separating groups admittedly closely allied, such as annelids and arthropods, and echinoderms and Branchiotremata, is futile and confusing." Yet she accepts Aschelminthes as a phylum under which she lumps the Rotifera, Gastrotricha, Kinorhyncha, Nematoda, Nematomorpha, and Acanthocephala as classes. By definition, the Aschelminthes have "Intestine more or less straight, anus posterior, no anterior ciliated projection except in a few rotifers." By this definition, the one negative character of "no anterior ciliated projections" is the single possible basis for including the Acanthocephala under this concept. Furthermore, it seems to the writer that more than "a few" of the rotifers have "anterior ciliated projections."

Morphology and morphological nomenclature have been particularly unfortunate in the extent to which isolated workers on little known groups have developed wholly unique descriptive and morphological terms without adequate understanding of the relations of the structures concerned to structures in other groups. Both multiplication of terms for identical structures and application of identical terms to unrelated structures have arisen from this lack of coordination. In the past, there have been crusaders who have attempted to carry on a one-man revolution for uniformity, proposing the junking of all the divergent morphological nomenclature in favor of one uniform series of terms applicable to all groups. A good example was A. D. MacGillivray's well-intentioned attempt at standardization of terminology in insect morphology which, despite its logic and its fundamentally sound basis, never gained any considerable following. In a more limited manner, Miss Hyman has proposed many revolutionary changes in the present volume, some of which may secure a following but doubtless many of her proposals will little influence practice of zoologists who fail to appreciate the need for yet another change to end all further change. "Epidermis" and "gastrodermis" seem like perfectly logical terms but it is hardly probable that they will ever replace "ectoderm" and "entoderm," even if the latter do carry an embryonic connotation. In fact, after proposing gastrodermis on page 264 the author lapses into the use of the familiar "entodermal epithelium" on page 280 and on page 232 suggests that the two cell layer in Mesozoa "do not correspond to the ectoderm and entoderm of Metazoa."

The mechanics of phylogenetic origin of syconid from asconid type of sponge are pushed rather hard in the statement (page 289) that the syconid "is formed by the outpushing of the wall of an asconid sponge at regular intervals into finger-like projections, called radial canals." An opportunity for expressing the creative urge was overlooked when the author refers repeatedly to "hatching" of sponge gemmules.

The section dealing with recapitulation (page 272) is particularly well written, even though the point of view here advanced is opposed by many embryologists. The sentence "Every ontogeny is a compromise between an inherited ancestral mode of development and adaptive modifications and adjustments" is particularly well expressed.

In her consideration of the Protozoa, the author has adopted the now fairly popular interpretation of Protozoa as acellular animals but often lapses into familiar reference to cells, as, e.g., (pages 105, 248) in speaking of colonial flagellates she describes them as consisting of cells and (page 45) admits that "some of the colonial Protozoa are practically multicellular organisms."

Accepting the Doflein grouping of the classes of Protozoa into two subphyla based on the presence or absence of cilia, the author (page 47) has relied wholly on presence of cilia as the one means of diagnosing the Ciliophora and neglects consideration of the fact that cilia and flagella are morphologically identical.

In characterizing the flatworms (page 33), absence of an anus is the only feature invoked to distinguish them from the nemertines, despite the fact that the literature includes more than incidental reference to instances of an anus among the trematodes.

In explaining cephalization (page 253), no account is taken of the important role of the anterior migration of the mouth from a primitively mid-ventral to terminal position with attendant correlated effect on longitudinal condensation of the pre-oral nervous elements in the formation of the brain.

The criticisms voiced in the foregoing paragraphs are, in the main, minor and over-emphasis on points of this sort would be farthest from the reviewer's intention. Dr. Hyman has incurred the gratitude of all zoologists interested in the invertebrates. Her publishers have maintained the same excellence of production which has distinguished their series of "Publications in the Zoological Sciences." It is sincerely hoped that Dr. Hyman will continue with her proposed series of volumes covering the remainder of the groups of the Invertebrates.—H. J. Van Cleave.

The Branchiobdellidae (Oligochaeta) of North American Crayfishes. By Clarence James Goodnight. 75 pp. 3 pl. Illinois Biological Monographs, vol. XVII, no. 3. $1.00.

There is a great need of precise morphological and taxonomic study of the smaller invertebrates of North America. The present work is a welcome contribution in this field. Following a brief historical resumé, there is an account of the morphology drawn chiefly from the literature. Characters of taxonomic importance are discussed. There is a detailed description of all known North American species of the family but as stated by the author only a few localities have been studied. The author divides the family into two new subfamilies: Branchiobdellinae for Branchiobdella, and Cambarincolinae for all other genera. Four new species are described, two in a new genus Triannulata. A brief discussion of the biology indicates a lack of host specificity for these ectocommensals of crayfish; the food consists chiefly of diatoms. The article suffers from a lack of illustrations which are limited to drawings of the new species.—L. H. Hyman.

Fleas of Eastern United States. By Irving Fox. Iowa State College Press, Ames, Iowa, 1940. vii + 191 pp., 31 pls. (166 figs.). $3.00.

Entomologists in general and public health workers in particular will welcome the publication of the present volume which is the first attempt since 1904 to gather together under one cover descriptions and illustrations of all known species of fleas inhabiting the United States east of the 100th meridian. It was in 1904 that C. F. Baker published his monographic contribution to our knowledge of North American Siphonaptera. In the intervening thirty-six years many small papers describing new genera and species have appeared and for this reason the taxonomy of the Siphonaptera has become difficult, especially for the beginning student.

At present, thirty-three genera including fifty-five species distributed among two suborders and five families are known for the region under discussion. One new genus for an aberrant species of bat flea is proposed. Keys to suborders and families are given in the opening pages of the work; keys to genera and species appear in proper sequence through the book. Each genus and species is adequately described and illustrated. The illustrations are not in the text, where they would be of most use, but are grouped on plates in the back of the volume. Indexes of synonyms, hosts, and fleas and a short but reasonably complete bibliography are included. This work undoubtedly fills a long felt want and a companion volume on the fleas of the West Coast and Rocky Mountain region would now be in order.—Edward A. Chapin.

Some Memories of a Paleontologist. By William Berryman Scott. Princeton University Press, Princeton, 1939. v + 336 pp., frontispiece of the author as he appears to-day. $3.75.

The Princeton University Press on September 2, 1939, published this very interesting volume. It deals with a man who has spent an active life, done much in his own particular field of science, traveled extensively and associated with most of the distinguished scientists of Europe and America. He describes his life among the people of the places visited by him, the Far West in the early days, Europe, South Africa and South America, revealing the joys and sorrows, relatively few, of a man of high culture,

education and scientific attainment. The nature of the book is so well summarized in the preface that it seems worth while to quote it in full:

"This book is the greatly reduced version of an autobiography which I wrote as a family record for my children. It seemed worth while to prepare an abbreviated story for publication, as recording a side of American life which is systematically ignored by our younger writers and of which Europeans seem to be entirely ignorant. Some one has said that autobiography is necessarily fiction, but I repudiate that judgment for myself. It is, of course, necessary to make a selection of facts out of an immense store of memories and records, but I have honestly endeavoured to make the selection with perfect fairness. The story is but a sketch, but an undistorted one. I have a good memory, nothing phenomenal, but still trustworthy, and there is before me a very long series of letters, written to my wife, both before and after our marriage. These letters, supplemented by diaries, have enabled me to make out an unusually complete narrative, in which the dates are but rarely uncertain. Whatever error of fact or opinion these chapters may contain, they are not fiction in any sense.

"I count myself to have had a fortunate and interesting life; the griefs and sorrows, of which I have had a full share, have been due to the loss of those dear to me. I have no grievances to exploit, or enemies to belabour; nevertheless, if I have succeeded in fairly transcribing my story, it can hardly fail to be an interesting one, because of the people that I have known and the places which I have visited."

He gives a vivid picture of Princeton University under various presidents of whom perhaps the most interesting to the reader is Woodrow Wilson. As a young Princeton student Scott was a baseball enthusiast and no mean player. His remarks on modern college athletics are interesting, and worthy of consideration.

Notables of all classes are mentioned in these Memories, even Bill Nye and his description of the North Platte River, "a mile wide and an inch deep." His first European contacts were with Huxley and Balfour. His Ph.D., acquired at Heidelberg, necessarily brought him into contact with many German scientists; and his description of German university life was to the reviewer very interesting. One of his comments is of especial interest at the present time, his reference to a reprimand he received from Professor Gegenbaur, under whom he was doing his chief work, because he had told another German some of the results of his own observations. The Germans seem to have had little trust in each other.

The great South American paleontologist, Ameghino, the inventor of such eccentric generic names as *Oldfieldthomasia*, is, according to Scott, a really distinguished scientist, in spite of many views to the contrary.

Marsh, the bête noire of American paleontologists, was frankly disliked by Scott as well as by others, although his ability as a paleontologist is recognized by him. Little praiseworthy is said of him, either in print or by word of mouth. The reviewer, however, as a schoolboy, once had the pleasure of meeting Marsh on a Cheyenne and Northern Railroad train. To the schoolboy, bound for Fort Laramie, armed with a shotgun and small collecting case, Marsh, at that time (1889) appeared to be a very affable and friendly old gentleman who took a great interest in the birds a youth expected to collect. Marsh, a few years previously, published his large quarto on extinct toothed American birds, and told him how a copy might be obtained, which was promptly done. Fort Laramie was probably the "neglected and ill kept" military post that Scott describes, but the eyes of a boy found it a delightfully interesting place.

The International Zoological Congress, which met in Boston in the summer of 1907, brings forth a remark from Scott which is all too true: "As I have usually found to be the case, the principal value of the Congress was in its social side, in the opportunity to see old friends again and to make new acquaintances among men whose work has long been familiar. Of the papers and discussions, I have but the vaguest recollection."

The book illustrates three important factors in the life of a scientist: the selection of good heredity, a sound education and continued diligence in the prosecution of his chosen field of work. To one who wishes to gain an insight into the life of one of our great scientists and college professors as well as an insight into the life of the Far

West in early days, of England in the days of Huxley, of Germany at her intellectual zenith, and of Princeton University, the book will appeal most profundly. It is not without interest that "Wick" Scott, the author's familiar name, is a brother of General Hugh L. Scott, U. S. A., who has published *Memories* of his own.

The volume concludes with 13 pages of an excellent and well prepared index.

—MARCUS W. LYON, JR.

FLORA OF KANSAS. By Frank C. Gates. Agricultural Experiment Station, Kansas State College, Manhattan, Kansas, 1940. 266 pp., 80 pls., 2 maps.

A new state flora is always a matter of interest to anyone concerned either with the systematics or the phytogeography of the flora of North America. After twenty years of assiduous collecting and study, Prof. Frank C. Gates has produced a "Flora of Kansas," containing an annotated list of the flowering plants and ferns of the state with maps showing the distribution of most species.

The first 21 pages comprise an introduction to the history and ecology of the flora, problems involved, statistical table of the families, acknowledgements, and a very short bibliography. The lucid description of the topographic divisions, climate, and habitats, in conjunction with the distributional maps, local habitats, and growth-form data are the author's major contribution in this work to American botany. It is only to be regretted that space limitations in a book of this character prevent a more definite localization of stations on the map than to the county. Concerning the acknowledgements, one cannot forbear pointing out that A. S. Hitchcock (until his death), Mrs. Agnes Chase (until her recent retirement), S. F. Blake, and J. R. Swallen should be associated with the Bureau of Plant Industry, rather than with the National Herbarium, and that F. J. Hermann has been for the last two years on the staff of the Bureau of Plant Industry, rather than of the University of Michigan. It might also be noted that although Dr. Hermann is mentioned as contributor of the sections on Juncaceae and Carex, he did not write these portions of the book. They were taken with some alterations from papers he had previously published on these groups from Kansas, and the names used are not always in agreement with those in the original papers or with Dr. Hermann's present concepts.

The section from page 21 to page 101 is made up of the series of distribution maps, with explanatory material and additional citations. For the user's benefit it would have been of interest to have one large map of the state accompanying these smaller maps with the names of the counties plainly visible. County names cannot be read, even with a lens, in the maps as they appear.

The annnotated list, pages 104-254, is the main body of the book. There are no keys or descriptions. The family arrangement is that of Bessey with some modification by the author. The adoption of this system seems a bit unfortunate in that it makes the genera very hard to find without recourse to the index. While admitting that Bessey had a keen discernment for relationships in certain instances, it is obvious that the system is not sufficiently superior to the Engler or Bentham and Hooker systems to justify use in a manual. It seems better to use one of the familiar systems until a new one appears that is so obviously superior that it necessarily commands wide acceptance.

One is impressed throughout the list with certain obvious though rather unimportant inconsistencies, such as the use of various abbreviations of the same author's name (Wats. or S. Wats., Mack. or Mackenzie, Fern. or Fernald, etc.), and the formal inclusion of cultivated plants in some families, with only incidental mention of others at the ends of their families.

The main object of this rather lengthy review, however, is to protest against the careless taxonomic and especially nomenclatorial practices with which the book is replete.

The author claims (p. 13) to be following the International Rules, yet at least four rejected names, *Syndesmon*, *Calceolaria*, *Neomamillaria*, and *Ptiloria*, are used, while in other cases, *Dalea*, *Broussonetia*, *Amphicarpa*, *Desmodium*, etc., the conserved names are used.

To Britton and Rose are ascribed (pp. 217-218) the four combinations used in *Neomammillaria*, though these species were treated by Britton and Rose in the quite distinct genus *Coryphantha* (and its seggregate *Neobesseya*) (Cactaceae 4: 43, 52, 53, 1923). Nelson is given (p. 221) as authority for *Elaeagnus argentea* (Nutt.) A. Nelson. In his article combining the genera *Shepherdia* and *Elaeagnus* Nelson actually made no such combination, which is a later homonym of *E. argentea* Pursh, but renamed the plant *Elaeagnus utilis* A. Nels. All five of these inadvertent new combinations are fortunately invalid because of omission of the name-bringing synonym or at least its reference.

Fernald (Rhodora 42: 266-267, 1940) has taken the author to task for the use of simple trinomials with no designation as to whether they are subspecies or varieties. On p. 16 Gates calls them varieties, but various combinations originally made as subspecies (*Atriplex patula* subsp. *hastata* (L.) Hall & Clements, *Descurainia pinnata* subsp. *brachycarpa* (Richardson) Detling [not Detlinger], etc.) are sprinkled through the list with nothing to distinguish them from the many that were made as varieties.

In his designation of hybrids, Gates has in most cases adopted a method which goes the rules one better. Instead of one X he uses two (X *Viola papilionacea* x *scroria*). For some hybrids (as X *Prunus slavini* Palmer) he uses a simple binomial with an X. What is meant by (p. 111) X *Tradescantia tharpii* x *(T. bracteata)* is not clear.

On page 13 the author announces that no attempt will be made to go into the synonymy of the plants, except where the name used differs from that used in the popular manuals of the region. In carrying out this policy the author makes no distinction between synonymy and plain misidentification. This gives rise to such misleading errors as the Linnean species *Lilium canadense* in synonymy under *L. michiganense* Farwell, *Rubus argutus* Link, under *R. ostryifolia* Rydb., *Juncus tenuis* Willd. under *J. macer* S. F. Gray, *Potentilla canadensis* L. under *P. simplex* Michx., *Svida amonum* [sic] (Mill.) [no auth.] under *Cornus obliqua* Raf., *Malva rotundifolia* L. both as a good species and as a synonym. *Commelina nudiflora* is given as a synonym of *C. longicaulis* Jacq., though it is actually a synonym of *Aneilema nudiflora*, and has been long confused with *C. diffusa* Burm. Authorities for synonyms are given or omitted evidently at random. Parenthetical authorities are sometimes given, sometimes omitted. In several instances the parenthetical authority is given but the other omitted.

Wrong names are used for several species, for example, *Myriophyllum proserpinacoides* Gill. (1833) is antedated by *M. brasiliense* Camb. (1829). *Juncus aristulatus* Michx. should be (acc. F. J. Hermann) *J. biflorus* Ell., and *Vaccaria vulgaris* Host has at least two earlier names in *Vaccaria*, but should probably be retained in *Saponaria* as *S. vaccaria* L. The synonym given under this species, *Saponaria vulgaris L.* was, so far as I am aware, never published by Linnaeus.

A minor point may be noted in the spellings "puncturvine" (p. 151), "addertung" and "adder's tung" (p. 104) (but on p. 108 "white adder's-tongue").

Last, but by no means least, may be mentioned the casual treatment of higher categories. The "Superfamily Compositae" (p. 232) is neither described nor justified. How it differs from the "Order Asterales" (p. 20) is not explained. The "Order Rubiaceae" has a family termination. Of course there is plenty of unfortunate precedent for irresponsible renaming of orders and even of families. It seems to me that the renaming of an order or family is a matter of much more importance, even, than renaming a genus or species, and should be as carefully considered.

Of course, these nomenclatorial slips are of little consequence to the professional botanist, who will merely ignore them, but it should be remembered that the chief users of any state flora are students and amateurs, who are very likely to follow any practices sanctioned by such an authority as the author of the book. If taxonomic usage, in general, is to be improved, the first step should be correct practice in books that will be used by students.—F. R. Fosberg, Bureau of Plant Industry, Washington, D. C.